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Review Paper

Biochemical cycling of nitrogen and phosphorus in biochar-amended soils

Shamim Gul [a, b], Joann K. Whalen [a, *]

[a] Department of Natural Resource Sciences, Macdonald Campus, McGill University, 21 111 Lakeshore Road, Ste-Anne-de-Bellevue, Quebec, H9X 3V9, Canada
[b] Department of Botany, University of Balochistan, Saryab Road, Quetta, Balochistan, Pakistan

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ABSTRACT

There is global interest in understanding the prospects for biochar application to agricultural soils. If biochar enhances the availability of nitrogen (N) and phosphorus (P) to crops, this could be pivotal in reducing N and P fertilizer inputs to agricultural soils. This review evaluates the soil biochemical cycling of N and P as influenced by biochars with diverse characteristics, and describes the consequences for plant nutrition with respect to the N use efficiency (NUE) and P use efficiency (PUE) of crops grown in biochar-amended soils. Fundamentally, biochar can alter microbial-mediated reactions in the soil N and P cycles, i.e. N_2 fixation, mineralization of N and P, nitrification, ammonia volatilization and denitrification. As well, biochar provides reactive surfaces where N and P ions are retained in soil microbial biomass and in exchange sites, both of which modulate N and P availability to crops. Distinctions must be made between biochars derived from manure- and crop residue-based feedstocks versus biochars derived from ligno-cellulosic feedstock, as well as biochars produced at a lower production temperature (<400 °C) versus biochars generated at a higher production temperature (≥ 600 °C). These factors determine the nutrient retention capacity of biochars when they are applied to soil. For example, low bioavailable N and P concentrations are expected when coarse-textured soil is amended with biochar having a high surface area, necessitating fertilizer application to avoid N and P deficiencies in the crop. Since the biochemical cycling of N and P in biochar-amended soil is affected strongly by biochar × soil interactions, detailed assessment of biochar-induced changes in soil physico-chemical properties and biological processes may improve predictions of how diverse biochars will affect soil fertility and crop nutrition under site-specific conditions.

1. Introduction

Most agricultural soils are limited in their ability to supply adequate N and P to crops, mainly due to the fact that the plant-available ionic forms of these nutrients are susceptible to loss via leaching (i.e., NO_3^- and the ortho-P ions $H_2PO_4^-$ and HPO_4^{2-}), conversion to gaseous forms (e.g., NH_3, NO, N_2O and N_2), and fixation or precipitation reactions (i.e., NH_4^+ fixation in clays, precipitation of ortho-P ions with calcium carbonate in alkaline soils and with aluminum and iron oxides in acidic soils). Inorganic N and P fertilizers are used to meet crop demands, but inefficient nutrient recovery from fertilizers has environmental consequences such as eutrophication, global acidification and global warming (Galloway et al., 2014). Rational use of inorganic N and P fertilizers requires consideration of the inherent reserves of plant-available N and P that are supplied to crops through internal recycling in the soil environment.

Biochar is a soil amendment with potential to improve N and P recycling in the soil-plant system. This carbonaceous solid residue is produced by heating biomass under oxygen-deficient conditions through slow and fast pyrolysis, gasification and hydrothermal carbonization. The latter three methods are suitable for energy and bio-oil generation at the industrial scale, whereas slow pyrolysis is a traditional method of charcoal production that generates more biochar than the other pyrolysis methods (Brewer and Brown, 2012). The important characteristics of pyrolyzed biochars affecting the biochemical cycling of N and P are: high surface area, pH and nutrient content. These characteristics vary among biochars depending on their source (feedstock) and production temperature. Manure- and crop residue-based biochars are richer in nutrients,

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* Corresponding author.
E-mail address: joann.whalen@mcgill.ca (J.K. Whalen).

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tend to have higher pH and greater surface area than the biochars produced from ligno-cellulosic feedstocks such as wood (Gul et al., 2015; Mohanty et al., 2013; Novak et al., 2013; Singh et al., 2010). Likewise, slow pyrolyzed biochars produced at a higher production temperature ($\geq$550 °C) tend to have greater surface area and higher pH values, but have lower plant-available nutrient concentrations than those produced at a lower production temperature (Al-Wabel et al., 2013; Cantrell et al., 2012; Mukherjee et al., 2011; Singh et al., 2010).

The diverse physico-chemical properties of biochar exert a variable influence on soil N and P cycling (Biederman and Harpole, 2013; Lehmann et al., 2011). Moreover, the soil physico-chemical properties affect the N and P cycling rates in biochar-amended soil (Biederman and Harpole, 2013; Lehmann et al., 2011). For instance, biochars that have greater surface area have greater adsorption capacity for ionic forms of N and P. Thus, biochars with low nutrient content (e.g., wood-based biochars) may be beneficial to reduce NO_3^- and ortho-P leaching in nutrient-rich soil, but their application in nutrient-poor soil may reduce the concentration of bioavailable N and P (Fig. 1) and have consequences for microbially-mediated reactions in the soil N and P cycles (Cayuela et al., 2013; Hussain et al., 2016; Lehmann et al., 2011). In contrast, biochars produced from manure feedstock have high pH values, 5–6 times greater nutrient content than residue-based biochars and >10 times higher nutrient content than wood-based biochars, and so are less likely to cause nutrient limitation in soil (Gul et al., 2015). However, high concentrations of base cations in some biochars can cause a significant increase in soil pH and contribute to soil salinity, which impaired crop growth in a poorly-buffered acidic soil (Sigua et al., 2016a) but had no negative impact on crop performance in well-buffered acidic soils (Murray et al., 2015; Subedi et al., 2016).

Biochar application to agricultural fields for soil fertility improvement is gathering momentum in many parts of the world (Jirka and Tomlinson, 2014). Generalizations about biochar performance must be balanced against the realization that biochars are highly heterogeneous in their form and reactivity in soil, which affects soil N and P dynamics, crop nutrition and yield. If a particular biochar can enhance internal N and P recycling in soil, it may also increase the N and P use efficiency of crops. Therefore, information on the biochemical cycling of N and P in the soil and plant compartments of biochar-amended agroecosystems is required to evaluate the prospect of using biochar to reduce our reliance on N and P fertilizer inputs. This fundamental knowledge is essential to develop guidelines for the selection and appropriate use of biochars to achieve desired agronomic outcomes.

The objective of this review is to examine how biochar types, determined by the feedstock source and production temperature affect (1) biochemical cycling of N, (2) biogeochemical cycling of P and (3) crop performance, namely N and P acquisition from biochar-amended soils. To compare data from diverse studies, we converted volumetric biochar applications (e.g., % or g biochar 100 g^{-1} soil) to a mass basis (i.e., t ha^{-1}) using the conversion factors of Ameloot et al. (2014) and indicate these estimated values with a tilde (~) symbol.

2. Nutrients in biochar

Biochars contain various organic and inorganic forms of N and P including NO_3^-, NH_4^+, ortho-P and amide groups (Kookana et al., 2011; Jindo et al., 2014). Concentration of these nutrients depends on the source and production temperature, as summarized by Gul et al. (2015). Biochars produced from nutrient-rich feedstocks like manure and crop residues generally have higher nutrient content than biochars generated from ligno-cellulosic feedstocks. Nitrogen forms in biochar are affected by the production temperature, such that biochars produced at higher temperatures have more NO_3^- while biochars produced at lower temperatures have more NH_4^+ (DeLuca et al., 2009). Azuara et al.

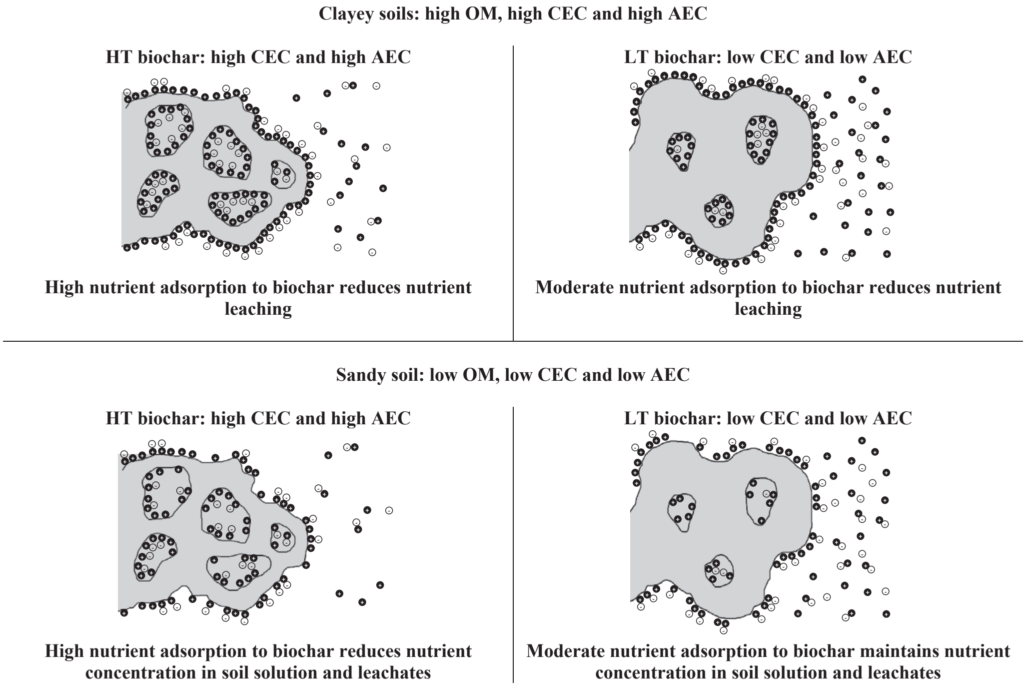

Fig. 1. Conceptual model of the cation exchange capacity in clayey (fine-textured) and sandy (coarse-textured) soils as influenced by slow pyrolyzed biochars produced at high and low production temperatures. The circles with + and − signs indicate cation and anions. The largest particle represents a soil organo-mineral surface while the smaller irregular greytone/hatched structures are biochar. OM: organic matter; CEC: cation exchange capacity; AEC: anion exchange capacity; HT: high production temperature; LT: low production temperature.

(2013) reported that ortho-P represented 60–75% of the total P in biochar produced from pig slurry by fast pyrolysis at 400–600 °C, whereas Mukherjee and Zimmerman (2013) found that ortho-P was 17–61% of the total P in wood-based biochars (slow pyrolyzed at 250 °C or 650 °C). The reduction in ortho-P concentration with increasing production temperature noted by Mukherjee and Zimmerman (2013) is consistent with the decline in bioavailable P concentration with increasing production temperature (from 300 to 700 °C with slow pyrolysis) reported for biochars made from pig manure, municipal solid waste and cotton crop residues (Zornoza et al., 2016). In summary, there is a net loss of plant-available N due to NH_3 volatilization with increasing production temperatures, and a decline in plant-available P concentration due to ortho-P crystallization with insoluble magnesic, ferric and calcic phosphates at higher pyrolysis temperatures (Zornoza et al., 2016).

3. Biochar-mediated effects on the soil nitrogen cycle

As most reactions in the soil N cycle are controlled by microorganisms, it is important to understand how microbial communities and their activities are modified in biochar-amended soils (Fig. 2). This is due to (1) direct effects, whereby biochar provides a niche for opportunistic microorganisms, and (2) indirect effects, such as the provision of labile substrates from fresh biochar, soil pH and moisture alteration, and sorption of signal molecules (Gul et al., 2015). The principles of sustainable agriculture suggest that crop production targets should be achieved with the lowest possible input of N fertilizer and greater reliance on internal N recycling (Gardner and Drinkwater, 2009), so the fundamental question is whether biochar amendments will be helpful in enhancing the microbially-mediated N transfer to crops. The next sections examine how biochar affects key microbial reactions in the soil N cycle: N acquisition through N_2 fixation, internal N recycling through organic N mineralization and nitrification, and N losses from the system through denitrification and NH_3 volatilization.

3.1. Biological N_2 fixation

Globally, biological N_2 fixation (BNF) is responsible for supplying 2.95 Tg N y^{-1} to pulse crops and about 18.5 Tg N y^{-1} for oilseed legumes through the action of free-living and symbiotic bacteria possessing the nitrogenase enzyme (Herridge et al., 2008). Enhanced BNF in biochar-amended soils was reported in many studies, particularly when slow pyrolyzed biochar was used (Mia et al., 2014; Ogawa and Okimori, 2010; Rondon et al., 2007). Mia et al. (2014) found that biochar produced from grassland shoot biomass (slow pyrolyzed at 400 °C) and applied at ~10 t ha^{-1} and ~50 t ha^{-1} to soil of unspecified texture in pots resulted in 39–45% more nodules g^{-1} root of red clover (*Trifolium pratense* L.) and increased N_2 fixation by 56% with ~10 t ha^{-1} and by 48% with ~50 t ha^{-1} of biochar amendment. There was 31% greater N_2 fixation by *Rhizobium* strains associated with bean plants grown in pots with clay loam soil that was amended with ~15 t ha^{-1} of *Eucalyptus deglupta* wood biochar (slow pyrolyzed at 350 °C) (Rondon et al., 2007). Quilliam et al. (2013) studied BNF in a sandy loam soil from agricultural fields amended with wood-based biochar (slow pyrolyzed at 450 °C) at rates of 25 + 25 t ha^{-1} and 50 + 50 t ha^{-1} in the previous three years. Biochar increased the soil pH from 6.3 to 7.2. Clover planted in pots containing biochar-amended soil had greater K and Na uptake, 35.4% more root nodule dry weight, and nitrogenase activity increased by 63% per nodule in the 25 + 25 t ha^{-1} treatment to 74% per nodule in the 50 + 50 t ha^{-1} treatment after 35 d (Quilliam et al., 2013). Expression of the *nifH* gene expression increased by 9% after one month and by 12% after six months in a coarse silty soil amended with switchgrass biochar (slow pyrolyzed at 450 °C) (Ducey et al., 2013). However, green waste biochar produced at 700 °C and mixed with a loamy sand soil had no influence on the *nifH* gene after 86 d incubation (Harter et al., 2014). Together, the evidence from pot and field studies suggests that slow pyrolysis biochar produced at 350–450 °C stimulates the activity of symbiotic bacteria responsible for BNF in leguminous plants grown on coarse- and fine-textured soils.

In their review, Mia et al. (2014) proposed six mechanisms whereby biochar could enhance BNF in leguminous plants: 1) by increasing the soil pH, 2) due to greater P bioavailability, 3) by immobilizing inorganic N, 4) through the input of macro- and micro-nutrients from biochar, 5) by increasing nodulation, and 6) by adsorbing Nod factors and flavonoids, which increases chemical signaling between the host and symbiont. The effect of various biochars on soil pH, P bioavailability and inorganic N concentrations were summarized by Gul et al. (2015), but mechanisms 4–6 merit discussion. Macro- and micro-nutrients that can stimulate

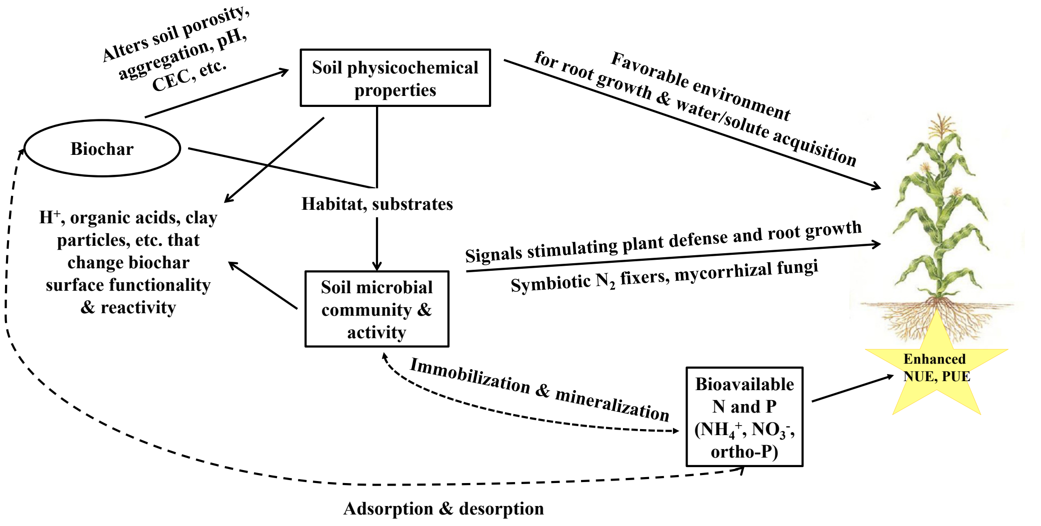

Fig. 2. Conceptual model illustrating the influence of biochar on soil physico-chemical and biological properties, and the consequences for crop root growth and nutrient acquisition from soil. NUE: nitrogen use efficiency; PUE: phosphorus use efficiency.

BNF are P, K, Fe and Mo (Vitousek et al., 2002), all of which may be present in biochar. For instance, Oram et al. (2014) suggested that the K input increased BNF of red clover grown on biochar-amended soil. Mechanisms 5 and 6 should be related because nodulation requires induction of nodule formation by Nod factors and flavonoids. If these signal molecules are adsorbed by biochar, as reported by Masiello et al. (2013) for wood-based biochar (slow pyrolyzed at 700 °C), this would interfere with the cell-to-cell communication that is necessary to induce nodule formation. Adsorption of signal molecules and other charged ions in biochar-amended soil is quantifiable, since it is a function of the reactive surface area of the biochar and associated soil organo-minerals (DeLuca et al., 2009). Mechanisms 5 and 6 could be tested experimentally by measuring nodulation and signal molecule production of leguminous plants grown in soil amended with biochars having variable surface area. It would be informative to consider biochar × soil interactions by including coarse- and fine-textured soils in future studies.

3.2. Organic N mineralization

Free-living soil microorganisms responsible for organic N mineralization are influenced by biochar × soil interactions. A particular biochar may stimulate, have no influence or negatively affect organic N mineralization in soil (Maestrini et al., 2014; Prayogo et al., 2014; Prommer et al., 2014). For instance, organic N mineralization was stimulated by 7% in a sandy loam soil mixed with ~8 t ha^{-1} of wheat straw biochar (slow pyrolyzed at 525 °C), while biochar produced from the same feedstock by fast pyrolysis caused a 43% reduction in the inorganic N concentration in the same soil type during a 65 d incubation period (Bruun et al., 2012). Fast pyrolyzed biochar had 62.5% higher surface area than slow pyrolyzed biochar, so either more inorganic N was adsorbed to the biochar surface or more N immobilization occurred in microbial cells that colonized the biochar surface. Biochars produced from ligno-cellulosic feedstocks with low nutrient content are expected to cause net N immobilization in the short-term, while those produced from nutrient-rich manure or crop residues may stimulate organic N mineralization (Ameloot et al., 2015; Zimmerman et al., 2011). For example, Cely et al. (2014) reported that net N mineralization was 12% lower in soil amended with ~128 t ha^{-1} of wood-based biochar (slow pyrolyzed at 620 °C) than the unamended sandy loam soil. In the same study, there was 35% greater net N mineralization in soil mixed with ~128 t ha^{-1} of paper sludge + wheat husk biochar (slow pyrolyzed at 500 °C) and 5% more net N mineralization in soil blended with sewage sludge biochar (slow pyrolyzed at 600 °C) after 45 d incubation.

The influence of biochar source and production temperature on organic N mineralization will be modulated by soil properties. As discussed by Ameloot et al. (2015), soil containing higher soil organic matter (SOM) or dissolved organic carbon (DOC) concentrations is likely to support organic N mineralization when amended with biochar. In fact, short-term immobilization of N following biochar amendment is not necessarily negative for crop production, since N will eventually be released through microbial turnover due to physical disruption (e.g., wet-dry and freeze-thaw cycles), predation or starvation when C-rich substrates are depleted. Understanding the biochar-mediated effects on organic N mineralization in relation to soil properties such as the SOM content could be helpful in deciding when (e.g., in spring or fall) and what type of biochar to apply (e.g., biochar produced from ligno-cellulosic versus manure feedstocks; biochar produced at low versus high production temperature). For example, biochars produced from ligno-cellulosic feedstock and/or at high production temperatures tend to retain inorganic N through adsorption and immobilization, so their application in autumn might be effective in preventing NO_3^- loss during winter months, particularly in coarse-textured soils (Fig. 1). In spring, a shift from net immobilization to net mineralization would release inorganic N to partially meet crop N demands in biochar-amended soil. Judicious use of supplemental fertilizer, such as organic fertilizer containing labile C that stimulates N mineralization or inorganic N fertilizer added to overcome temporary immobilization, would improve the N fertility status of such biochar-amended soils (Sigua et al., 2016b).

3.3. Ammonia volatilization

Ammonia volatilization is a major pathway for N loss from agricultural soils worldwide, particularly when ammonia-based fertilizer (i.e., urea) is applied (Macnack et al., 2013). About 10% of urea-N fertilizer is lost annually through NH_3 volatilization in subtropical agroecosystems of India (Datta et al., 2012), while 26% of N fertilizer (most commonly urea) is volatilized as NH_3 from summer maize agroecosystems in China (Wang et al., 2014). The major edaphic factors responsible for NH_3 volatilization are high pH, soil moisture content and higher soil temperatures (Macnack et al., 2013).

There is consensus that biochar reduces NH_3 loss from soils. The mechanisms responsible for this phenomenon are: 1) adsorption of NH_3 to biochar (Spokas et al., 2012; Taghizadeh-Toosi et al., 2012a), which depends on biochar surface area and enhanced CEC of biochar-amended soil (Clough and Condron, 2010; Clough et al., 2013), and 2) adsorption of NH_4^+, which prevents its conversion to gaseous NH_3 (Chen et al., 2013; Malinska et al., 2014; Mandal et al., 2016; Spokas et al., 2012; Steiner et al., 2010; Taghizadeh-Toosi et al., 2011, 2012a). In their review, Clough and Condron (2010) explained that NH_3 adsorption also depends on the presence of acid functional groups on biochar surfaces, which decline as the biochar production temperature increases. However, high production temperature increases the biochar surface area and promotes greater CEC if the biochar is activated or as biochar is gradually oxidized, which is expected to facilitate NH_3 and NH_4^+ adsorption in biochar-amended soil (Clough and Condron, 2010). In soils with diverse SOM and pH values, Mandal et al. (2016) found up to ~70% reduction in NH_3 volatilization from urea-N fertilizer following amendment with poultry litter biochar (slow pyrolyzed at 550 °C) and Macadamia nut shell biochar (slow pyrolyzed at 460 °C), which they attributed to NH_3 adsorption by biochar, immobilization and nitrification.

Alkaline biochars often increase soil pH, which could trigger NH_3 volatilization. However, there was a 45% reduction in NH_3 volatilization from ^{15}N-labelled ruminant urine (10 g N L^{-1}) added to a silt loam soil (pH 5.5) that was mixed with 15 or 30 t ha^{-1} of pine wood biochar (slow pyrolyzed at 350 °C; pH 7.77) during a 29 d incubation (Taghizadeh-Toosi et al., 2011). As pine wood biochar had high retention capacity for NH_4^+, it was determined that NH_4^+ absorption by the biochar resulted in the lower NH_3 emissions (Taghizadeh-Toosi et al., 2012b). We conclude that biochar application to agricultural soil will often prevent NH_3 volatilization from ammonia-based fertilizers, although the effectiveness of biochar in this regard will depend on its surface area and reactivity (i.e., presence of acid functional groups).

3.4. Nitrification

In well-aerated agricultural soils, NH_4^+ undergoes rapid oxidation and nitrification to NO_3^- when there is an ample NH_4^+ and soil pH is in the neutral to alkaline range. Due to its capacity to adsorb NH_4^+, biochar tends to reduce the NH_4^+ concentration in soil solution that is available to ammonium oxidizers. The decrease in soluble NH_4^+ concentration with increasing application rates of wood-based biochar was apparently responsible for the lower nitrification rates in biochar-amended soils (Taghizadeh-Toosi et al., 2012a). In contrast, biochars increased nitrification in soils that also received inorganic and organic N fertilizers (Berglund et al., 2004; Case et al., 2012; Kolb et al., 2009; Prommer et al., 2014; Ulyett et al., 2014; Zhao et al., 2014) or had higher SOM content (70–84 g organic C kg^{-1} soil; Hu et al., 2014; Song et al., 2014). Biochar application negatively influenced NH_4^+ oxidation when no N fertilizer was added and soil had a low SOM content (12–28 g organic C kg^{-1} soil; Angst et al., 2014; Ippolito et al., 2016; Zhang et al., 2015; Zheng et al., 2013), although this does not always occur in unfertilized soil with low C content (e.g., Angst et al., 2014; Kelly et al., 2015; Maestrini et al., 2014). These results seem to suggest that biochar exerts a direct effect on the activity of ammonia oxidizers and nitrifiers by altering NH_4^+ availability. However, biochar-induced changes in soil pH and other physico-chemical properties could affect the functions of ammonia oxidizers and nitrifiers at a community level. Such abiotic changes can affect the competitive ability of soil bacteria, archaea and fungi that catalyze the ammonia oxidation and nitrification reactions, a topic that has received some attention (e.g., Song et al., 2014) but warrants further study in biochar-amended soils.

3.5. Denitrification

Denitrification, the microbial reduction of NO_3^- into N_2 with several intermediates (i.e., NO_2^-, NO, N_2O) is the major biological reaction producing N_2O in temporarily waterlogged soils, with additional N_2O released from the nitrifier-denitrification pathway in aerobic soils (e.g., at 50% water-filled pore space; Kool et al., 2011). A comprehensive review of biochar and N_2O emissions by Cayuela et al. (2014) confirms that the feedstock source, pyrolysis temperature and C:N ratio of biochar, as well as biochar interactions with soil texture and N fertilizer, influence N_2O loss from biochar-amended soils. In general, biochar-amended soils have lower N_2O emissions and more N_2O reduction to N_2 (Alburquerque et al., 2015; Easton et al., 2015; Wang et al., 2013; Zwieten et al., 2014). Biochar affects soil N_2O emissions by altering the NO_3^- and DOC concentrations, soil pH and soil moisture content (Cayuela et al., 2014). Biochar can reduce N_2O production by 1) enhancing NO_3^- immobilization in microbial biomass and uptake by plants, as demonstrated by several authors (e.g., Deenik et al., 2011; Dempster et al., 2012; Maestrini et al., 2014; Prayogo et al., 2014; Zheng et al., 2012), 2) increasing soil pH (Firestone et al., 1980; Gul et al., 2015), 3) promoting soil aeration by reducing bulk density and increasing porosity (Gul et al., 2015), and 4) increasing *nosZ* gene expression (Anderson et al., 2011; Cayuela et al., 2013; Harter et al., 2014), which encodes the nitrous oxide reductase that reduces N_2O to N_2.

There is considerable evidence that N_2O mitigation depends on biochar × soil interactions. For instance, there was 56% more N_2O emitted from nutrient-rich sandy loam soil amended with ~30 t ha^{-1} green waste biochar (slow pyrolyzed at 550 °C) than the unamended control, while a nutrient-poor loamy sand soil showed 76% reduction in N_2O emission with the same biochar and application rate, compared to the unamended control, during a 14 d incubation (Sanchez-Garcia et al., 2014). The nutrient-rich soil in their study had 69% greater NO_3^- and 37% higher DOC concentrations than the nutrient-poor soil. A negative relationship between the C:N ratio of biochar and N_2O production was also reported (Cayuela et al., 2013, 2014) and more N_2O reduction to N_2 occurred in fine-textured than coarse-textured soils (Table 1). The retention of N_2O in soil micropores facilitates its reduction to N_2 (Maag and Vinther, 1996), and this effect could be enhanced when biochar micropores are colonized by denitrifiers, or when the micropores act as a trap for N_2O and prevent its diffusion to macropores that emit soil air to the atmosphere. This mechanistic interpretation could explain the general trend of lower N_2O emissions and more N_2O reduction to N_2 in biochar-amended soils. Still, these findings offer little insight into how biochar-amended soils may mitigate N_2O emissions in the field, where considerable spatial heterogeneity and temporal fluctuations in denitrification are expected.

4. Biochar-mediated effects on the soil phosphorus cycle

Bioavailable P (i.e., ortho-P) is produced in the soil biogeochemical cycle through organic P hydrolysis and inorganic phosphate solubilization, mediated by the action of free-living microorganisms, root symbionts and plant roots that produce hydrolytic enzymes and organic acids. Ortho-P in the soil solution may diffuse to the nearby plant roots or be intercepted by the high-affinity transporters of arbuscular mycorrhizal fungi, which then transfer it to the host plant. Biochar amendments can alter these hydrolysis and solubilization reactions, as well as ortho-P transport by mycorrhiza, as discussed in the following sections.

4.1. Organic P hydrolysis

Organic P hydrolysis is carried out by extracellular enzymes (i.e., phosphatase, phytase, phospholipase) produced by plant roots and soil microorganisms. As enzyme activity and microbial biomass are the most important determinants of P mineralization (Bohme et al., 2005), Masto et al. (2013) asserted that biochar enhances P mineralization by increasing microbial biomass. The evidence to support this claim comes from the ~3 times greater microbial biomass and ~19% increase in phosphatase activity after 20 d in a soil of unspecified texture that was amended with ~3.5 t ha^{-1} of biochar produced from water hyacinth (*Eichornia crassipes*) biomass by slow pyrolysis at 300 °C (Masto et al., 2013). There is a general expectation of greater microbial biomass carbon (MBC) concentrations in biochar-amended soils (Lehmann et al., 2011), modulated by biochar × soil interactions (Gul et al., 2015). In particular, the soil MBC concentration tends to be higher with biochars produced from manure or crop residues than wood-based biochars (Ameloot et al., 2013, 2014; Domene et al., 2014; Kolb et al., 2009; Maestrini et al., 2014; Mitchell et al., 2015; Rutigliano et al., 2011). As summarized by Gul et al. (2015), the MBC concentration increased from 12.5% to 83% across a range of fine-textured to coarse-textured soils that were amended with ~8–160 t ha^{-1} of manure- and crop residue-based slow pyrolysis biochars (production temperatures 350–700 °C). Since larger microbial biomass demands more ortho-P to sustain its metabolic functions, according to the principles of stoichiometric homeostasis, this supports the claim of Masto et al. (2013) that biochar-amended soil with a high MBC concentration will also have a high P mineralization rate.

Soil pH modification is another way that biochar affects P hydrolysis, with higher soil pH values reported to enhance alkaline phosphatase activity (Du et al., 2014; Jin et al., 2016). In their study, Du et al. (2014) reported ~2 to ~3 times increase in alkaline phosphatase activity in the 0–5 cm depth of a sandy loam soil under winter wheat and summer maize rotation that received four annual applications (9 t ha^{-1} y^{-1}) of corncob biochar (production temperature of 360 °C). Similarly, the 28.5% greater alkaline phosphomonoesterase activity in a clay loam soil coincided with an increase in soil pH from 6.9 to 7.5 following application of 25 t ha^{-1} of swine manure biochar (slow pyrolyzed at 400 °C), and the alkaline phosphomonoesterase activity nearly doubled in a silt loam soil that was amended with the same biochar source and rate, which increased the pH from 5.2 to 5.8 during a 98 d incubation (Jin et al., 2016). The acid phosphomonoesterase activity declined in both

Table 1
Physical and chemical characteristics of soils, % reduction in N_2O production and % increase in N_2 production following biochar application, compared to unamended control soils (values are pooled among 5 biochar types). Chemical characteristics of biochar are provided in the lower section of the Table. All biochar-soil mixtures were incubated at 90% water filled pore space during a 40 d incubation period (data from Cayuela et al., 2013).

Soil name	Soil texture	Bulk density (kg dm^{-3})	DOC[a] (mg kg^{-1})	DON[b] (mg kg^{-1})	NO_3^- (mg kg^{-1})	NH_4^+ (mg kg^{-1})	% reduction in N_2O production	% Increase in N_2 production
Arkport	Sandy loam	1.55	156	12	4	18	67	−69
Coronella	Clay loam	1.34	142	n.d.[c]	3	492	90	−84
Costa	Silt clay loam	1.28	219	135	11	1077	80	45
Hudson A	Silt loam	1.38	174	8	8	4	18	0
Lentiscosa	Sandy clay	1.33	64	n.d.	2	31	31	86
Lins	Sandy loam	1.55	54	n.d.	7	16	−38	0
Niagara	Silt loam	1.39	85	1	3	78	72	61
Secanos	Loam	1.35	125	2	3	96	75	−85

Biochar chemical characteristics

Biochar type	Organic C (%)	N (mg kg^{-1})	C:N	Surface area (m^2 g^{-1})
Bamboo wood	60.5	5.5	110	126
Dairy manure	51.2	21.0	24.4	13
Grass clipping	53.5	49.5	10.8	50
Mixed wood chip	85.9	3.7	231	–
Oak wood	83.9	1.9	450	176

[a] DOC, dissolved organic carbon.
[b] DON, dissolved organic nitrogen.
[c] n.d., not determined.

soils (Jin et al., 2016), suggesting a possible shift in the soil microbial community composition that might be attributed to the pH buffering or nutrient input from the swine manure biochar. We conclude that biochar application favors organic P hydrolysis in soil, but whether this is due to greater ortho-P demand and extracellular enzyme production by the soil microbial community, or due to soil pH modification that increases the activity of alkaline phosphatase, remains to be confirmed.

4.2. *Arbuscular mycorrhizal fungi*

The association between crop plants and mycorrhizal fungi is well known to enhance P uptake by crops through the combined action of plants and fungi in secreting extracellular phosphatases and phosphate solubilizing organic acids. Due to the ability of fungal hyphae to enter microsites that are inaccessible to plant roots, mycorrhiza are highly efficient at acquiring P and transporting it to the host plant (Warnock et al., 2007). Biochar is frequently found to promote mycorrhizal colonization of host crops (e.g., Blackwell et al., 2010; Mahmood et al., 2003; Matsubara et al., 2002; Miller et al., 2002; Rondon et al., 2007; Saito, 1989; Yamato et al., 2006). Using ^{33}P tracer and electron microscopy, Hammer et al. (2014) found that AM fungi *Rhizophagus irregularis* was strongly attached to outer and inner narrow surfaces of nutrient-loaded wood biochar (550 °C), resulting in six times more ^{33}P translocation to the host plant *Daucus carota* compared to experimental units where mesh halted hyphal colonization of biochar.

In their reviews, Warnock et al. (2007) and Atkinson et al. (2010) considered that biochars promote mycorrhizal colonization of plant roots by providing refugia to mycorrhizal fungi and by enhancing the growth of P solubilizing bacteria that co-occur with mycorrhiza. However, two separate meta-analyses made by Lehmann et al. (2011) and Biederman and Harpole (2013) and empirical evidence (e.g., Birk et al., 2009; Warnock et al., 2010) leads to the conclusion that less mycorrhizal colonization will occur in nutrient-rich soil amended with biochar. This idea is consistent with the accepted knowledge that high soil fertility reduces plant dependence on mycorrhizal fungi for nutrient acquisition and leads to the hypothesis that more mycorrhizal colonization will occur in nutrient-poor soil amended with wood-based biochar (Fig. 3). This concept is supported by the observation that greater mycorrhizal colonization of wheat roots (from 1.4 to 16%) and higher wheat biomass (~7–8 times more dry weight) occurred when a nutrient-poor loamy sand soil was amended with 5 t ha^{-1} of various biochars, compared to the unamended control (Blackwell et al., 2015). Biochars in this study were produced from *Acacia saligna* wood (slow pyrolyzed at 380 °C) and *Eucalyptus marginata* wood (slow pyrolyzed at 550–650 °C) mixed in a 10:1 ratio (biochar:fertilizer) with beneficial microbe-inoculated inorganic fertilizer (N, P, K, S, Ca, Mg with microbial inoculation at 750 g t^{-1} fertilizer). Interpreting results from Blackwell et al. (2015) is difficult due to the complexity of interacting factors introduced in the experiment, i.e., various biochar feedstocks and production temperatures, supplemental nutrients and microbial inoculants. It does illustrate the need to consider how biochar affects the soil physico-chemical and biological properties that are important for the development of mycorrhiza.

4.3. *P solubilizing microorganisms*

Plant roots, plant growth promoting rhizobacteria and arbuscular mycorrhizal fungi secrete organic acids (e.g., gluconic, oxalic, citric, acetic and succinic acids) that solubilize ortho-P from secondary minerals and organo-mineral surfaces (Antoun, 2012: Vassilev et al., 2013). In their review, Vassilev et al. (2013) suggested that nutrients contained in biochar ash enhanced microbial secretions of P solubilizing acids and concluded that animal bone biochar was a sustainable substitute for inorganic P fertilizer. He et al. (2014) achieved 47–54% greater solubilization of added ortho-P by inoculating ~8 t ha^{-1} rice husk biochar (production temperature not specified) with the organic acid-producing bacteria *Lysinibacillus sphaericus* and *Lysinibacillus fusiformis* in a growth medium. Mendes et al. (2014) reported approximately three-fold higher ortho-P solubilization from phosphorus rock (containing 13.97 P and 1.59% F^-) when mixed with holm oak biochar (slow pyrolyzed at 480 °C) at a 1:1 phosphate rock:biochar ratio and applied to the potato dextrose agar growth medium (pH 7) inoculated with *Aspergillus niger*. There was ~2 fold increase in citric and gluconic acid and ~3.5 fold increase in oxalic acid production from *Aspergillus niger*, compared to the control, and biochar adsorbed

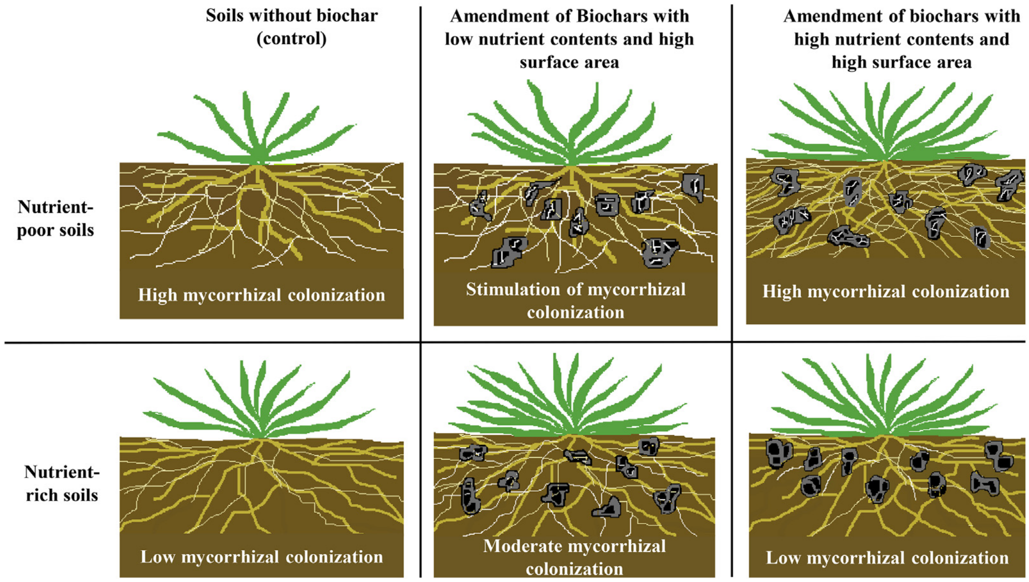

Fig. 3. Hypothetical model showing mycorrhizal colonization of plants grown in nutrient-poor and nutrient-rich soils. When nutrient-poor soil is amended with biochar containing high surface area and low nutrient content (e.g., wood-based biochars produced at high production temperatures), the reduction in bioavailable nutrient concentration will stimulates mycorrhizal colonization. In nutrient-rich soil, such biochar types enhance mycorrhizal colonization. Likewise, biochar with high nutrient content and high surface area (e.g., biochars produced from manure and crop residue feedstocks) results in high mycorrhizal colonization in nutrient-poor soil and low mycorrhizal colonization in nutrient-rich soil.  is biochar particles. The thin white lines superimposed upon the plant roots indicate mycorrhizal hyphae.

33% of the F^- ions, which was sufficient to overcome barriers to phosphate solubilization. Nutrient-loaded biochar increased the production of organic acids capable of solubilizing ortho-P, with a greater response in nutrient-poor than nutrient-rich soils (Deb et al., 2016). These preliminary findings from controlled environments indicate the potential of biochar to stimulate the activity of P solubilizing microorganisms, but further studies are needed in realistic soil environments to confirm the prospects for biochar in this regard.

5. Crop performance for N and P acquisition in biochar-amended soils

5.1. *Root growth*

Biochar is often reported to improve root growth. For instance, the root growth of spring barley increased significantly in a coarse-textured soil amended with ~32 t ha^{-1} of hardwood biochar (slow pyrolyzed at 450–480 °C) (Bruun et al., 2014). Root growth of winter wheat increased by 36% with pine chip biochar and by 44% with hardwood biochar (both produced by slow pyrolysis at 350 °C) when 40 t ha^{-1} of these biochars were applied to a loamy sand soil (Sigua et al., 2016a). There was ~34% higher root length intensity in an apple orchard where wood biochar (slow pyrolyzed at 500 °C) was applied at 10 t ha^{-1} to a silty clay loam soil (Ventura et al., 2014). Enhanced root growth in biochar-amended soils may be attributed to the nutrient input from biochar. For instance, Prendergast-Miller et al. (2014) reported that *Miscanthus* biochar (slow pyrolyzed at 700 °C) was responsible for a 29% increase in root biomass and 14% greater rhizosphere circumference in spring barley, as well as 27% greater root P uptake than the control, while *Salix* wood biochar (slow pyrolyzed at 450 °C) had no significant effect on any of these parameters. The *Miscanthus* biochar had ~2 times more labile C and ash, and ~7 times more extractable P than the *Salix* wood biochar.

Although the nutrient input from ash associated with biochar is generally positive for root growth, biochar-amended soils with high salt concentrations can cause osmotic stress in roots. This was the case when Sigua et al. (2016a) applied 40 t ha^{-1} of poultry litter biochar (slow pyrolyzed at 350 °C) to a loamy sand soil and observed 86% reduction of winter wheat root biomass. Poultry litter biochar contained a high concentration of soluble salts, notably 2.2% Na, 6.9% K, 4.9% Ca and 1.9% Mg (Sigua et al., 2016a). Such high salt concentrations could raise the electrical conductivity past the tolerance range (about 8 dS m^{-1}) for winter wheat (Wentz, 2001), particularly since watering was carefully controlled in the pot study of Sigua et al. (2016a) and there was apparently little opportunity for excess salts to be leached. Moreover, base cations present in the poultry litter biochar increased soil pH from 4.9 to 8.4, which may have affected the solubility and uptake of essential plant nutrients. While the pot study of Sigua et al. (2016a) may suggest it is inadvisable to apply poultry litter biochar to coarse-textured, acidic soils with limited buffering capacity, further study is needed to determine whether such precautions are necessary under field conditions.

5.2. *N and P use efficiency*

Rational use of inorganic fertilizers should be cost-effective and efficient, with minimal nutrient loss to the environment. This can be achieved by increasing the nutrient use efficiency of crops, which is defined as the ability of crops to acquire soil nutrients and incorporate them in plant organs (i.e., root and shoot biomass, leaves, seeds and fruits) (Baligar et al., 2001). Biochar application is expected to enhance the NUE of plants, including grain and oilseed crops (Table 2) as well as horticultural, tuber/root and pasture crops

Table 2
A summary of cereal grain, legume grain, maize and oilseed crop production, N and P uptake in biochar amended soils. The biochar source, production temperature and application (Appl.) rates are provided. The yield (YD) gain or loss (% difference from 0 t ha^{-1} biochar amendment) and nitrogen use efficiency (NUE) parameters of crops (1) nutrient efficiency ratio (NER) calculated as biomass (or yield)/nitrogen contents in tissue and agronomic efficiency (AE) calculated as yield under treatment − yield under control/nitrogen fertilizer applied (Baligar et al., 2001).

Biochar: Source and production temperature (°C), frequency of application	Appl. rate of biochar (t ha^{-1})	Soil texture	Soil pH	N fert. (kg ha^{-1})	P fert. kg ha^{-1})	Crop and experiment method (pot or field)	Yield (grain/ fruit in t ha^{-1})	% YD than cont.	N uptake (kg ha^{-1})	P uptake (kg ha^{-1})	NUE parameters (kg kg^{-1} N fertilizer)		Reference
											NER	AE	
Straw (730 °C)	0	Coarse sandy	6.5	208	29.7	Barley (pot)	0.96		–	–	–	–	Bruun et al. (2014)
	8						1.02	6.0	–	–	–	0.0002	
	16						1.20*	20	–	–	–	0.0011	
	32						0.85	−11.5	–	–	–	−0.0005	
	64						0.69	−28.2	–	–	–	−0.0013	
Wood (450–480 °C)	32						1.06	9.50	–	–	–	0.0004	
Debarked spruce chips (500 –600 °C)	0	Clay loam	6.6	0	0	Faba bean (field)	3.32		–	–	–	–	Tammeorg et al. (2014a)
	5						3.27	−1.51	–	–	–	–	
	10						3.28	−1.21	–	–	–	–	
Willow wood (550 °C)	0	Red Ferrosol (clayey soil)	5.6	34.5	37.5	Maize (field)	7.14		–	–	–	–	Agegnehu et al. (2016)
	10			34.5	37.5		9.21*	22.5	–	–	–	0.0600	
Wood (–[a])	0	Sandy loam	–	100	100	Maize (field)	5.8		–	–	–	–	Kimetu et al. (2008)
	6						6.9*	16	–	–	–	0.0110	
	0	Clay loam	–	100	100		5.8	0	–	–	–	–	
	6						6.1*	5	–	–	–	0.0030	
– First year (Biochar applied at once in the beginning over 4 years study)	0	Clay loam	3.9	–	–	Maize (field)	5		137	19	0.036	–	Major et al. (2010)
	8						5	0	139	22	0.035	–	
	20						5	0	138	14	0.036	–	
Second year	0						5		121	18.5	0.041	–	
	8						**6**	17	138	20.5	0.043	–	
	20						**6.5***	23	**147***	**24.7***	0.044	–	
Third year	0						5.8	14	130	16	0.044	–	
	8						**6.7***	25.4	140	23	0.047	–	
	20						**7.8***	36	**143***	**24***	0.054	–	
Fourth year	0						1.9		30.2	6	0.063	–	
	8						**3.3***	42.5	–	–	–	–	
	20						**4.3***	55.8	**60.8***	**13***	0.070	–	
Herbaceous weed (350 –550 °C)	0	Sandy loam	5.9	100	60	Maize (field)	3.59		–	–	–		Masto et al. (2013)
	4						**4.0***	10.3	–	–	–	0.004	
Rice husk (350–550 °C)	0	Sandy loam	4.2	250	250	Maize (field)	1.3		–	–	–		Mekuria et al. (2014)
	10						2.2	61	–	–	–	0.0036	
	0	Loamy sand	5.4				2.1	38.1	–	–	–	0.0032	
	10						2.3	43.5	–	–	–	0.0040	
Cow manure (500 °C)	0	Sandy	6.4	60	26.2	Maize (pot)	1.3		31.8	2.85	0.041		Uzoma et al. (2011)
	15						**3.2***	59.4	**67.1***	**8.98***	0.047	0.032	
	20						**2.4***	46	**63.8***	**7.84***	0.037	0.018	
Giant reed (–)	0	Silt loam	6.2	600	600	Maize (pot)	–		–	–	0.57	–	Zheng et al. (2013)
	16						–		–	–	**0.94***	–	
	32						–		–	–	**1.02***	–	
	80						–		–	–	**1.18***	–	
Hardwood (450–500 °C) (Pool result of three years)	0	Silty	6.4	–	–	Maize (pot experiment under field conditions)	0.76		–	–	–	–	Borchard et al. (2014)
	24						0.41	−46.1	–	–	–	–	
	160						**0.25***	−67.1	–	–	–	–	
Willow wood (550 °C)	0	Loamy sand	6.2	26.6	31.6	Peanut (field)	4.17		–	–	–		

	10						5.05	17.5	–	–	–	0.033	Agegnehu et al. (2015)
Wheat straw (350–550 °C)	0	Red soil	4.5	90	0	Rapeseed (field)	0.0014		–	–	–		Liu et al. (2014)
	2.5						**0.0017***	17.7	–	–	–	0.0003	
	20						**0.0019***	26.3	–	–	–	0.0005	
	40						**0.0025***	32.0	–	–	–	0.0012	
Wood residue (350–550 °C)	0	Clay loam	5.4	0	0	Rice (field)	0.7		–	–	–	–	Asai et al. (2009)
	8						0.8	12.5	–	–	–	–	
	18						0.7	0	–	–	–	–	
	0	Loam		0	0		3.8		–	–	–	–	
	8						4.0	5.0	–	–	–	–	
	16						3.7	−2.6	–	–	–	–	
Wheat straw (400 °C)	0	Sandy loam		0	0	Rice (pot)	0.96		0.86	–	1.116	–	Xie et al. (2013)
	12			0	0		0.60	−37.5	0.88	–	0.68	–	
	12			250	0		**1.35***	29.0	0.83	–	1.626	0.0030	
	0	Clay loam		0	0		0.41		0.81	–	0.506	–	
	12			0	0		0.32	−21.2	0.71	–	0.450	–	
	12			250	0		0.42	2.4	0.86	–	0.488	0.0004	
Wood (–) first year	0	Clayey soil		30	35	Sorghum (field)	0.28		4.7	–	0.059		Steiner et al. (2008)
	11			30	35		0.42	34	7.1	–	0.059	0.0046	
Second year	0			30	35		0.14		2.3	–	0.061		
	11			30	35		0.28	50	4.6	–	0.061	0.0766	
Sawdust of trees (300–350 °C)	0	Clayey soil	8.8	0	0	Soybean (BATISoybean5 variety)	0.4		–	–	–		Mete et al. (2015)
	20			0	0		**0.7***	43.0	–	–	–		
	20			60	175		**2.1***	81.0	–	–	–	0.0230	
	0			0	0	Soybean (BINA soybean 1 variety)	0.49		–	–	–		
	20			0	0		**0.75***	34.7	–	–	–		
	20			60	175		**2.3***	78.7	–	–	–	0.0258	
	0			0	0	Soybean (Shohag (PB-1) variety)	0.52		–	–	–		
	20			0	0		0.7	26.0	–	–	–		
	20			60	175		**1.9***	72.6	–	–	–	0.0200	
Beech wood	0	Silt loam	7.4	120	0	Spring barley (field)	5.5		155	20.1	0.035		Karer et al. (2013)
	24						5.4	−2.0	151	18.9	0.036	−0.00008	
	72						**6.0***	8.4	160	21.4	0.038	0.0042	
	72			0	0		4.8	−13	98	12.8	0.049	−0.0056	
Maize silage (600 °C)	0	Loamy sand	6.2	0	–	Spring wheat	1.12		–	–	–		Reibe et al. (2015)
	65			0	–		1.08	−3.6	–	–	–		
	65			160	–		**4.22***	73.5	–	–	–	0.0196	
Wood chip (850 °C)	90			0	–		1.01	−9.8	–	–	–		
	90			160	–		**3.92***	71.4	–	–	–	0.0181	
Five biochar types, each for a given individual treatment: olive stone (507 °C), almond shell (472 °C), wheat straw (368 °C), pine woodchips (428 °C), olive-tree pruning (449 °C)	0	Loamy sand	6.5	0	0	Sunflower (pot)	Yield not significantly different than control for all the treatments						Alburquerque et al. (2014)
	8												
	40												
	80												
	120												
Horticultural charcoal from coppiced woodlands (500 °C)	0	Silty sand loam	5.2	122	50	Wheat (field)	2.28		–	–	–		Vaccari et al. (2011)
	30						**2.92***	22.0	–	–	–	0.0052	
	60						**2.93***	22.2	–	–	–	0.0053	

(continued on next page)

Table 2 (*continued*)

Biochar: Source and production temperature (°C), frequency of application	Appl. rate of biochar (t ha^{-1})	Soil texture	Soil pH	N fert. (kg ha^{-1})	P fert. kg ha^{-1})	Crop and experiment method (pot or field)	Yield (grain/ fruit in t ha^{-1})	% YD than cont.	N uptake (kg ha^{-1})	P uptake (kg ha^{-1})	NUE parameters (kg kg^{-1} N fertilizer) NER	NUE parameters (kg kg^{-1} N fertilizer) AE	Reference
Second year (biochar was applied once in first year)	0						2.40		–	–	–	0.00009	
	30						**3.19***	24.7	–	–	–	0.0075	
	60						**3.34***	28.1	–	–	–	0.0087	
Olive tree pruning (450 °C)	0	Clay loam	8.2	110	0	Wheat (field)	4.42		–	–	–		Olmo et al. (2014)
	40						**5.61***	21.22	–	–	–	0.0110	
Debarked spruce chips (500 –600 °C)	0	Loamy sand	4.6	63.4	0	Wheat (field)	3.8		–	–	–		Tammeorg et al. (2014b)
	5						3.5	−8.0	–	–	–	−0.0047	
	10						3.6	−5.3	–	–	–	−0.0032	
	20						3.4	−10.5	–	–	–	−0.0063	
	30						4.1		–	–	–	0.0047	
Debarked spruce chips (500 –600 °C)	0	Clay loam	6.6	0	0	Wheat (field)	6.67		–	–	–	–	Tammeorg et al. (2014a)
	5						6.33	−5.1	–	–	–	–	
	10						6.43	−3.6	–	–	–	–	

Values in bold and followed with * are significantly different than control treatment ($P < 0.05$).

[a] Represents no data or not applicable.

(Table 3), particularly when high rates of biochar are applied. The NUE of crops is also predicted to be greater when biochar is co-applied with inorganic fertilizer and compost (Alburquerque et al., 2013; Doan et al., 2015; Schulz and Glaser, 2012; Schulz et al., 2013; Steiner et al., 2008). However, it is difficult to support these expectations with data from the literature. Although crops yields are often evaluated in biochar-amended soils under field conditions (22 of the 32 studies reported in Tables 2 and 3), the crop N uptake was measured about 20% of the time (in 5 of 23 studies reported in Table 2; in 2 of 10 studies shown in Table 3). The few data available on NUE in biochar-amended soils are from field and pot studies. Despite our best efforts, we were not able to find a single report of PUE although data exists on the P uptake by maize, spring barley, ryegrass and radish in biochar-amended soils (Tables 2 and 3).

The data we compiled for this review shows that the yield of grain and oilseed crops was improved with biochar application in a variety of soil types (Table 2). Biochar application rates that induced positive yield response could be as low as 2.5 t ha^{-1} (Liu et al., 2014) or as high as 72 t ha^{-1} (Karer et al., 2013). Meta-analysis by Crane-Droesch et al. (2013) found that 3 t ha^{-1} of biochar caused and increase in average crop yield, whereas Jeffery et al. (2011) found the greatest yield gain was achieved in soil amended with 100 t ha^{-1} of biochar. In our analysis, 14 out of 23 studies showed positive crop performance in response to biochar amendment (Table 2). Out of these 14 studies, 7 studies were done in coarse-textured soil while the rest were done in fine-textured soil. Improved crop yield in fine-textured soils receiving biochar is counter to the findings of Jeffery et al. (2011) and Crane-Droesch et al. (2013), who reported a weak association between clay content and crop yield gain in biochar-amended soil.

We contend that biochar did not improve crop performance unless co-applied with inorganic fertilizers (Table 2). Biochar applications of ~8–80 t ha^{-1} plus inorganic fertilizers enhanced crop yield significantly ($P < 0.05$) by 5–81% during the first year of cropping, with no apparent difference in crop responses between coarse- and fine-textured soils. This finding is in contrast to Crane-Droesch et al. (2013), who found little evidence of crop yield improvement when inorganic N fertilizer was added to biochar amended soils. Further, we present evidence in Table 2 that biochars produced from manure or crop residue feedstocks can promote crop yield and N uptake during the first year of cropping, especially in fine-textured soils. In contrast, the wood-based biochars produced at higher temperatures tend to reduce crop yield in coarse-textured soils during the first year of cropping (see also Butnan et al., 2015). Our findings support the co-application of NPK fertilizer or organic fertilizer to maintain crop yield during the first growing season after biochars from ligno-cellulosic feedstocks are applied to coarse-textured soils, which is consistent with the conclusions of Brown et al. (2011).

Similar results were found when we evaluated the performance of horticultural, tuber/root and pasture crops in biochar-amended soils (Table 3). Without inorganic fertilizers, only two studies showed a positive influence of biochar on crop yield during the first cropping season (Slavich et al., 2013; Mete et al., 2015) and one study demonstrated a significant ($P < 0.05$) increase in crop P uptake, which was ~2–4 times greater than the control (Chan et al., 2008). Both Slavich et al. (2013) and Chan et al. (2008) used biochars produced from manure-based feedstocks in fine-textured soils, conditions that are not expected to be nutrient-limiting for crop growth. Without inorganic fertilizer application, it is evident from Table 3 that biochar amendment did not increase crop yield in coarse-textured soils (e.g., Alburquerque et al., 2014; Reibe et al., 2015; Tammeorg et al., 2014a,b; Xie et al., 2013).

Table 3

A summary of horticultural, tuber/root and pasture crop production, N and P uptake in biochar amended soils. The biochar source, production temperature and application (Appl.) rates are provided. The yield (YD) gain or loss (% difference from 0 t ha^{-1} biochar amendment) and nitrogen use efficiency (NUE) parameters of crops (1) nutrient efficiency ratio (NER) calculated as biomass (or yield)/nitrogen contents in tissue and agronomic efficiency (AE) calculated as yield under treatment − yield under control/nitrogen fertilizer applied (Baligar et al., 2001).

Biochar: Source and production temperature (°C), frequency of application	Appl. rate of biochar (t ha^{-1})	Soil texture	Soil pH	N fetil. (kg ha^{-1})	P fertil. (kg ha^{-1})	Crop and experiment method (pot or field)	Yield (grain/fruit in t ha^{-1})	% YD than cont.	N uptake	P uptake	NUE parameters (kg kg^{-1} N)		Reference
											NER	AE	
Wheat straw (400 °C)	0	Silt clay	5.1	0	0	Amaranth (vegetable: *Amaranthus mangostanus*) (field)	20		–	–	–		Li et al. (2015)
	20			0	0		23*	13	–	–	–		
	40			0	0		20	0	–	–	–		
	0			104.2	104.2		18	−10	–	–	–		
	20			104.2	104.2		22.5*	12	–	–	–	0.043	
	40			104.2	104.2		17.5	−12.5	–	–	–	−0.0048	
	0			130.3	130.3		15.8	−21	–	–	–		
	20			130.3	130.3		23.5	15	–	–	–	0.0590	
	40			130.3	130.3		34*	42.2	–	–	–	0.1396	
Wheat straw (400 °C)	0	Silt clay	5.1	0	0	Baby Bok Choy (field)	20		–	–	–		Li et al. (2015)
	20			0	0		**35***	43	–	–	–		
	40			0	0		59	66.1	–	–	–		
	0			83	83		8	−60	–	–	–		
	20			83	83		**38***	47.4	–	–	–	0.3614	
	40			83	83		**60***	67	–	–	–	0.6265	
	0			145	145		23	13.1	–	–	–		
	20			145	145		25	20	–	–	–	0.0138	
	40			145	145		**40***	50	–	–	–	0.1172	
Wheat straw (400 °C)	0	Silt clay	5.1	0	0	Coriander (field)	23		–	–	–		Li et al. (2015)
	20			0	0		**28***	18	–	–	–		
	40			0	0		28.5	19.3	–	–	–		
	0			104.2	104.2		22.5	−2.2	–	–	–		
	20			104.2	104.2		28.5	19.3	–	–	–	0.0576	
	40			104.2	104.2		13.8	−40	–	–	–	−0.0835	
	0			130.3	130.3		25	8	–	–	–		
	20			130.3	130.3		24.7	6.8	–	–	–	−0.0029	
	40			130.3	130.3		**38.8***	40.7	–	–	–	0.1059	
Cattle feedlot manure (550 °C)	0	Red ferralsol	–[a]	0	0	Pasture (inter-cropped rye grass, clover, and summer forage peanut)	33		(N uptake for Rye grass) 21	(P uptake for Rye grass) 3.8	–	–	Slavich et al. (2013)
	–		–	–	–		34	3	22.6	4.3	–	–	
Municipal green waste manure (550 °C)	–		–	–	–		**35***	5.8	18	2.8	–	–	
Poultry litter (450 °C)	0	Loamy	4.6	0	0	Radish (pot)	2.1		13.2	1.46	0.159		Chan et al. (2008)
	25						3.4	38.3	13.4	**5.43***	0.254		
	50						3.8	46.2	13.2	**5.03***	0.288		
	0			100	0		3.4		22.8	1.13	0.149		
	25			100	0		5.3	36.0	17.0	**4.78***	0.312	0.0190	
	50			100	0		5.4	37.0	17.3	**4.95***	0.312	0.0200	
Poultry litter (550 °C)	0			0	0		2.1		12.8	1.94	0.164		
	25						3.3	36.4	14.8	**5.03***	0.223		
	50						4.3	51.2	15.4	**3.57***	0.279		
	0			100	0		3.8		17.7	1.29	0.215		
	25						6.0	37.0	18.3	**2.84***	0.328	0.0220	

(*continued on next page*)

Table 3 (*continued*)

Biochar: Source and production temperature (°C), frequency of application	Appl. rate of biochar (t ha^{-1})	Soil texture	Soil pH	N fetil. (kg ha^{-1})	P fertil. (kg ha^{-1})	Crop and experiment method (pot or field)	Yield (grain/ fruit in t ha^{-1})	% YD than cont.	N uptake	P uptake	NUE parameters (kg kg^{-1} N)		Reference
											NER	AE	
	50						6.5	41.5	20.3	**3.00***	0.320	0.0270	
Wheat straw (350–550 °C)	0	Red soil	4.5	90	0	Sweet potato (field)	0.0023		–	–	–		Liu et al. (2014)
	2.5						0.0022	−4.4	–	–	–	−0.000001	
	20						**0.0043***	46.5	–	–	–	0.00002	
	40						**0.0049***	53.1	–	–	–	0.00002	
Rice husk + cotton seed shell (400 °C)	0	Sandy loam	8.0	250	180	Tomato (pot)	27.5		–	–	–		Akhtar et al. (2014)
	80						**33.6***	18.2	–	–	–	0.0244	
Wheat straw (400 °C)	0	Silt clay	5.1	0	0	Tung Choy (field)	93		–	–	–		Li et al. (2015)
	20			0	0		**99***	8.2	–	–	–		
	40			0	0		77	−14.2	–	–	–		
	0			200	200		80	−13.3	–	–	–		
	20			200	200		**99.5***	7.4	–	–	–	0.0955	
	40			200	200		**181.5***	43.3	–	–	–	0.5075	
	0			350	350		104.2	6	–	–	–		
	20			350	350		96.5	−6	–	–	–	−0.0220	
	40			350	350		**107***	20	–	–	–	−0.0080	
Debarked spruce chips (500–600 °C)	0	Clay loam	6.6	0	0	Turnip Rape (field)	1.20		–	–	–	–	Tammeorg et al. (2014a)
	5						1.01	−15.8	–	–	–	–	
	10						1.13	−5.84	–	–	–	–	

Values in bold and followed with * are significantly different than control treatment ($P < 0.05$).

[a] Represents no data or not applicable.

6. Future directions

If biochar is to be a useful soil amendment, it should improve biochemical N and P cycling as illustrated in Fig. 2. This implies a comprehensive understanding of biochar × soil interactions that influence N and P cycling, including soil physico-chemical properties and biological responses of microorganisms and crops. Recommendations for future study are as follows:

- Biochar-induced changes in BNF need to be monitored before, during and after the crop growing season. This will provide information on how biochar amendment affects free-living versus symbiotic BNF activities. Moreover, BNF in the root nodules of leguminous crops need to be linked with the biochar-induced changes in root architecture, as well as in the number and size of the nodules. Signaling between N_2-fixing bacteria and roots in biochar-amended soils could be monitored using ^{13}C- and ^{15}N-based stable isotope techniques or by gas chromatography-mass spectrometry analysis of key signal molecules (e.g., flavonoids).
- Since the N mineralization rate in soil is a function of biological N demand (Pastor et al., 1984), a holistic approach that considers biochar-induced changes in microbial biomass, microbial N use efficiency, and crop growth (roots and aboveground biomass) will be helpful in establishing the biological N demand throughout the growing season. Although this is fairly easy to quantify in controlled laboratory studies, the challenge will be to consider how any change in N mineralization will affect immobilization, crop N uptake and NUE in biochar-amended soil under realistic field conditions.
- Efficient acquisition of NO_3^- by microorganisms and plants can reduce the NO_3^- concentration in soil microsites occupied by denitrifiers, leading to complete reduction of N_2O to N_2 and thereby mitigating soil N_2O emissions. The question to be answered is whether porosity and surface reactivity of biochar particles affects denitrification directly, or whether the change in N_2O emissions is the result of abiotic and biotic feedbacks in the soil-microbial-plant system of biochar-amended soils.
- Mechanisms explaining P mineralization rates in biochar-amended soils are unclear, necessitating further study of microbial biomass, microbial community structure and phosphatase enzyme activity. The hydrolytic activity of alkaline versus acid phosphatases in biochar-amended soils merits attention.
- The association between mycorrhizal fungal and host crops, which is essential for P acquisition in nutrient-poor soil, needs to be understood in relation to biochar applications. The hypothesized relationships shown in Fig. 3 should be tested experimentally to improve our understanding of mycorrhiza in biochar-amended soils.
- The observation that P enriched biochars derived from bones stimulate organic acid secretions by P-solubilizing microbes (Vassilev et al., 2013) raises an intriguing possibility that biochar could increase the solubilization of mineral-associated P. Ortho-P released from dissolution of P-rich secondary minerals, together with ortho-P mineralized from organic P, makes a major contribution to crop P fertility since the PUE from inorganic P fertilizers is generally less than 20% (Ziadi et al., 2013). How biochar affects the PUE from internal recycling of soil P reserves and from co-applied P fertilizers is not reported in the scientific literature at the present time.

7. Conclusions

The biochemical cycling of N and P in biochar-amended soil is affected by biochar characteristics such as its source and method of production, and by soil properties such as texture, pH and organic matter content. The capacity of biochar to adsorb gaseous N compounds and ionic forms of N appears to have a direct impact on NH_3 volatilization and denitrification. Other reactions in the soil N and P cycles seem to be affected by changes in soil physico-chemical properties, notably pH and nutrient content, and alteration of microbial community structure following biochar application. Crop root growth and yield are often enhanced with biochar, but little is known about the N and P uptake of crops grown in biochar-amended soil. Information on the NUE and PUE of field-grown agronomic and horticultural crops in soil receiving biochar or biochar co-applied with fertilizer is absolutely essential to determine the prospect of using biochar to reduce our reliance on N and P fertilizers in agriculture. At present, we have inadequate knowledge to develop guidelines on biochar use that are integrated with soil fertility and nutrient management planning. This is due to the fact that our understanding of N and P cycling in biochar-amended soil is based largely on pot experiments, which are suitable for mechanistic investigations. However, field studies are required to determine the magnitude of biochar-induced changes in N and P cycling and to link this to crop performance, particularly with respect to NUE and PUE.

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