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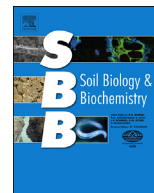

A mycorrhizal fungus grows on biochar and captures phosphorus from its surfaces

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ABSTRACT

Biochar application to soils has potential to simultaneously improve soil fertility and store carbon to aid climate change mitigation. While many studies have shown positive effects on plant yields, much less is known about the synergies between biochar and plant growth promoting microbes, such as mycorrhizal fungi. We present the first evidence that arbuscular mycorrhizal (AM) fungi can use biochar as a physical growth matrix and nutrient source. We used monoxenic cultures of the AM fungus *Rhizophagus irregularis* in symbiosis with carrot roots. Using scanning electron microscopy we observed that AM fungal hyphae grow on and into two contrasting types of biochar particles, strongly attaching to inner and outer surfaces. Loading a nutrient-poor biochar surface with nutrients stimulated hyphal colonization. We labeled biochar surfaces with ^{33}P radiotracer and found that hyphal contact to the biochar surfaces permitted uptake of ^{33}P and its subsequent translocation to the associated host roots. Direct access of fungal hyphae to biochar surfaces resulted in six times more ^{33}P translocation to the host roots than in systems where a mesh prevented hyphal contact with the biochar.

We conclude that AM fungal hyphae access microsites within biochar, that are too small for most plant roots to enter (<10 μm), and can hence mediate plant phosphorus uptake from the biochar. Thus, combined management of biochar and AM fungi could contribute to sustainable soil and climate management by providing both a carbon-stable nutrient reservoir and a symbiont that facilitates nutrient uptake from it.

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1. Introduction

Biochar is a carbon rich residue of pyrolyzed biomass (combusted under low oxygen conditions) that as a soil amendment can improve soil fertility. Many governments have recently become interested in investigation of biochar because of its potential in climate change mitigation (Laird, 2008; Sohi, 2012) because charcoal decomposes very slowly in the soil (estimates range from 1000 to 10,000 years; Skjemstad et al., 1998; Krull and Skjemstad, 2003). Soil organic carbon is globally the largest organic carbon reservoir, even when both the biosphere and the atmosphere are included (Lal, 2008). Transfer of carbon from the atmosphere to soil could thus have a large impact on the global carbon balance. Combining biochar production with bioenergy production could even result in a CO_2-negative balance (Lehmann, 2007a).

There are sites in South America where charcoal mixed with feces and bones has been added to soils over a period of several thousand years, resulting in e.g. the Amazonian Dark Earth, or *terra preta* soils. These soils have significantly higher fertility compared with nearby soils that lack charcoal, and the charcoal is considered at least partly responsible for this (Glaser et al., 2001).

Both in field observations and controlled experiments, plant yield has been observed to respond positively to biochar addition, especially in acidic and coarse textured soils (Jeffery et al., 2011).

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However, much less is known about the response of soil organisms to biochar addition (Lehmann et al., 2011), despite their importance for nutrient cycling and as plant symbionts. Mycorrhiza is a symbiosis between the majority of land plants and root endophytic fungi (Smith and Read, 2008). It is an ancient and ubiquitous mutualistic interaction that is important for plant biomass production. Among other functions in ecosystems (Rillig, 2004), mycorrhizal fungi provide their host plants with mineral nutrients and receive photosynthetically derived carbohydrates in return. Arbuscular mycorrhizal (AM) fungi are especially important for acquiring phosphorus (P), which has low mobility in soil and is often a poorly accessible plant nutrient because it is immobilized on soil colloids (Smith and Read, 2008).

The few studies of the effects of biochar on mycorrhiza have mainly considered root colonization and show diverging results. Some researchers report root colonization rates to be strongly enhanced by biochar (Ishii and Kadoya, 1994; Blackwell et al., 2010), whereas others present evidence that colonization decreases (Birk et al., 2009; Warnock et al., 2010). Some of the negative effects on root colonization could be explained by plant mediated feedback mechanisms, i.e. soils amended with high-ash biochar content could release and provide elevated amounts of available nutrients (Lehmann et al., 2003; Mukherjee and Zimmermann, 2013) and a nutrient-saturated host plant decreases its mycorrhizal root symbionts (Gryndler et al., 2006). It is likely that there are other, direct effects of biochar on mycorrhizal fungi that are poorly understood. To disentangle the direct effects from the indirect host-feedback effect, it is necessary to experimentally restrict the access to biochar to only the fungus.

Addition of biochar affects multiple soil properties that all can directly influence AM fungi (Warnock et al., 2007), such as: modified soil pH and its feedback on nutrient availability and microbial community structure (Lehmann, 2007b); altered nutrient release, retention or immobilization (Blackwell et al., 2010; Mukherjee and Zimmermann, 2013); changed water retention capacity (Glaser et al., 2002; Basso et al., 2013); and provision of shelter against fungivore grazing (Thies and Rillig, 2009; Ogawa and Okimori, 2010). The last could lead to a relative increase of viable hyphae inside biochar because intense grazing by soil animals decreases the amount of hyphae in the soil matrix. In the absence of grazing, increased hyphal density in the biochar must be a result of increased productivity, a foraging strategy in response to chemophysical properties of the material. It is known that AM fungi proliferate in both organic and inorganic nutrient rich patches (Hodge et al., 2001; Hammer et al., 2011).

Nutrients are taken up by AM fungi via active parts of the external mycelium, including the region immediately behind the growing hyphal tips (Bago, 2000). Older parts of the mycelium are also likely to be involved in nutrient uptake through lateral hyphal walls (Schnepf et al., 2007). Phosphorus is taken up as orthophosphate by high-affinity transporters in the external mycelium (Harrison and Van Buuren, 1995; Maldonado-Mendoza et al., 2001; Benedetto et al., 2005). Close proximity of the hyphae to the nutrient sources is important for uptake efficiency, especially for ions with low mobility such as phosphate (Barber, 1995).

The goals of our study were to investigate: a) whether AM fungal hyphae grow on and into ash-rich and ash-poor biochar and if this depends on the surrounding nutrient conditions; b) whether attachment and uptake structures are established on the biochar surfaces; and c) if AM fungi can acquire nutrients, especially P that is associated with biochar and thus whether biochar can serve as a nutrient reservoir. We used *in vitro* mycorrhizal cultures and added biochar in a separate compartment, to which hyphae, but not the host plant roots, had access. By using these gel/water-based cultures we could observe morphological patterns in the growth medium that otherwise are obscured in soil.

2. Materials and methods

2.1. Cultures and biochar

Experiments 1–3 were performed with sterile root organ cultures of *Daucus carota* L. inoculated with *Rhizophagus irregularis* Schenk and Smith (DAOM 197198; Biosystematics Research Center, Ottawa, Canada), recently recommended to be renamed from *Glomus intraradices* (Stockinger et al., 2009). Because of the biotrophic nature of AM fungi, sterile experiments need to be performed in connection with a host plant. To achieve this, transformed carrot roots with inhibited shoot formation were grown in Petri plates. The transformed *D. carota* roots originated from a clone of the DC1 line, transformed with T-DNA from the Ri plasmid of *Agrobacterium rhizogenes* (Becard and Fortin, 1988), originally established by StArnaud et al. (1996). Maintenance was accomplished by propagating AM fungi colonized cultures on a minimal nutrient medium (M-medium; Becard and Fortin, 1988; Table S1), including 10 g l^{-1} sucrose, low phosphorus concentration of 35 μM (4.8 mg l^{-1} KH_2PO_4) and 0.3% Phytagel™ for stabilization (Sigma Chemical Co., St. Louis, MO, USA). Experiments 1–3 used 2-compartmented Petri plates, where one side served as a root compartment (RC) including roots and the AM fungus, and the other served as a root free hyphal compartment (HC). The RC was filled with 15 ml M-medium containing phytagel and sucrose. Cylindrical plugs of colonized roots from four month old cultures were transferred into a hole in the fresh gel. After an establishment period of 30 days, the HC was filled either with 15 ml liquid M-medium lacking sucrose and phytagel, or with MilliQ water. Plates were produced in excess and only those were used that showed hyphal growth toward or over the barrier after 30 days, because a mycelium in the HC was the prerequisite for the start of the study. Roots passing over the barrier to the hyphal compartment were periodically removed.

We used a nutrient and ash poor wood biochar for Experiments 1–3. It was made from wood pellets, a mixture of spruce and pine wood without bark or any adhesive agents that are manufactured for household energy production (purchased from Bioenergi Skandinavien AB, Sweden). Pellets were cylindrical with a diameter of 0.7 cm and length of ~1.3 cm. They typically had an ash content of 0.3% and an N content of <0.1%. Biochar was produced by pyrolyzing the wood pellets at 550 °C under low oxygen conditions in a muffle furnace (Nabertherm, Wilhelm Tham AB, St Anna, Sweden) for 12 h. The pellet parent material was filled into metal containers, surrounded and covered by sand, and loosely sealed with aluminum foil. The resulting wood biochar was 0.5 cm in diameter and ~1 cm long; mass yield was 32% of the dry parent material. The wood biochar contained 85% C, 0.1% N (Euro EA Elemental Analyzer, HekaTech, Germany) and 0.15% P (acid digested in a 4:1 mixture (v:v)) of 65% nitric–70% perchloric acids; total P was determined by the molybdate blue method (Murphy and Riley, 1962, using Auto-Analyzer 3, Bran+Luebbe, Norderstedt, Germany). Ash content was 1.4%, determined gravimetrically after combustion at 600 °C. The pH of the wood biochar at equilibrium with water (1:5 w/w) was 7.6.

In Experiment 1, we also tested a nutrient- and ash-rich biochar that was produced from chicken manure (from Bauhaus, Econova Garden AB, S-61621 Åby, Sweden) under the same conditions as the wood pellet biochar. The chicken manure biochar product is coarsely granular, intermixed with sand particles and contains 37% C, 2.5% N and 0.5% P. Ash content was 44% and pH was 10.8. Biochar used in all experiments was derived from the

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