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Effects and mechanisms of biochar-microbe interactions in soil improvement and pollution remediation: A review☆

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ABSTRACT

Biochars have attracted tremendous attention due to their effects on soil improvement; they enhance carbon storage, soil fertility and quality, and contaminant (organic and heavy metal) immobilization and transformation. These effects could be achieved by modifying soil microbial habitats and (or) directly influencing microbial metabolisms, which together induce changes in microbial activity and microbial community structures. This review links microbial responses, including microbial activity, community structures and soil enzyme activities, with changes in soil properties caused by biochars. In particular, we summarized possible mechanisms that are involved in the effects that biochar-microbe interactions have on soil carbon sequestration and pollution remediation. Special attention has been paid to biochar effects on the formation and protection of soil aggregates, biochar adsorption of contaminants, biochar-mediated transformation of soil contaminants by microorganisms, and biochar-facilitated electron transfer between microbial cells and contaminants and soil organic matter. Certain reactive organic compounds and heavy metals in biochar may induce toxicity to soil microorganisms. Adsorption and hydrolysis of signaling molecules by biochar interrupts microbial interspecific communications, potentially altering soil microbial community structures. Further research is urged to verify the proposed mechanisms involved in biochar-microbiota interactions for soil remediation and improvement.

1. Introduction

For the purposes of soil remediation, biochar generally refers to a carbon-rich solid that is produced by the pyrolysis of biomass in oxygen-limited conditions (Beesley et al., 2011; Chen and Chen, 2009). Biochars are applied to soil due to their potential benefits for carbon sequestration, soil fertility, and contaminant immobilization (Cao et al., 2009; Chen et al., 2008a; Jeffery et al., 2015). The physiochemical properties of biochar are responsible for changes in soil character including changes in pH, nutrient maintenance, and water retention, which can induce heterogeneous responses in microbial species. This response can result in changes in microbial community structure and can consequently alter soil element cycling and function (Biederman and Harpole, 2013; Lauber et al., 2009; Rousk et al., 2009, 2010). There are some components in biochar, including minerals, volatile organic compounds (VOCs), and free radicals (Spokas et al., 2011), that can potentially influence microbial activity, reshape the soil microbial community, and change the soil enzyme activity that catalyzes various key biogeochemical processes including soil organic matter turnover and elemental cycles (e.g., N, P, and S) (Paz-Ferreiro et al., 2014). Due to the various positive effects on the soil properties and microbes, biochars are considered effective agents for soil remediation. However, the variability among different types of biochar makes its effects on soil remediation quite unpredictable, and the specific mechanisms of biochar-microbe interactions are still unclear.

The use of contaminant-degrading microbe inoculation (mycoremediation) together with biochar can enhance the biological degradation of pollutants (e.g., PAHs) (Chen and Ding, 2012; Chen et al., 2012a; Garcia-Delgado et al., 2015), providing a promising method for soil contaminant remediation. Such a process is considered a combination of the immobilization of the pollutants by the biochar and the further degradation of these pollutants by

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microbes. The adsorption of organic contaminants, toxic heavy metals, and hazardous anions (e.g., ClO_4^-) by biochar immobilizes them and prevents their leaching into the groundwater (Cao et al., 2009; Chen and Yuan, 2011; Chen et al., 2012d; Fang et al., 2014b; Jones et al., 2011; Yang et al., 2016b). Further transformation and detoxification of environmental pollutants by microbes as catalyzed by biochar have drawn increasing attention in recent studies (Dong et al., 2014; Oh et al., 2013). Persistent free radicals (PFRs) that are formed on biochar during thermal decomposition of the feedstocks activate reactive oxygen species (ROS) (Fang et al., 2015b; Kluepfel et al., 2014; Yu et al., 2015), and the electron transfer between biochar and microbial cells plays an important role in organic contaminant degradation and heavy metal transformation (Dong et al., 2014; Fang et al., 2015a; Yang et al., 2016a; Yu et al., 2015).

Biochar can participate in soil processes such as organic matter decomposition as it takes part in the direct extracellular electron transfer (DEET) between soil organic matter (or soil minerals) and microbial cells, as well as in the direct interspecific electron transfer between microbial cells (DIET) (Chen et al., 2014; Fang et al., 2014a). The identification and quantification of the reactive components of biochar particles that are responsible for the electron transfer between the biochar and soil microbes are essential to investigate biochar-involved elemental cycling. The electron transfer between biochar particles and soil minerals, organic matter, pollutant molecules, and microbial cells, as well as in response of the microbial community to the reactive components of the biochar, is an emerging research field that seeks to further clarify the effects of biochar on soil biogeochemical processes.

Several studies in the past decade extensively discussed the structure, physiochemical properties, and structure-function relationships of biochar with respect to the apparent effects of biochar on soil (Ahmad et al., 2014; Ameloot et al., 2013; Chen and Yuan, 2011; Chen et al., 2008a, 2012b; Lehmann et al., 2011; Warnock et al., 2007); however, an understanding of biochar-microbe interactions is a research gap that would link biochar properties with many soil processes, e.g., carbon storage and contaminant degradation. With regard to the newly found electron transfer and free radical activation functions of biochar, the mechanisms of biochar effects can be more clearly identified (Fang et al., 2015b; Kappler et al., 2014). Therefore, this review aims to seek answers for the following questions: (1) What are the most essential physiochemical properties of biochar that influence the microbial activity and community, and how do these properties influence the microbes? (2) Mechanistically, how does the interaction of the soil microbes with different types of biochar affect soil carbon sequestration and contaminant dissipation? Answers to these questions are essential to identifying the cause of the heterogeneous effects of biochar in existing research and to develop the required understanding to accurately predict biochar effects, both of which are key challenges in this research field.

2. Driving mechanisms of biochar-microbe interaction in soil

Biochar affects the soil microbial activity and biomass, changes the soil bacteria to fungi ratio and soil enzyme activity, and reshapes the microbial community structure (Ahmad et al., 2016; George et al., 2012; Mackie et al., 2015; Nielsen et al., 2014; Rutigliano et al., 2014). Note that biochar application may significantly alter the microbial community structure even when it does not change the overall microbial activity and biomass. To clearly interpret the microbial responses to biochar application in soils, gene copy numbers can serve as a more sensitive parameter than microbial biomass (Chen et al., 2013). Various techniques are used to test microbial activity and community structure, including ergosterol extraction, quantitative real-time polymerase chain reaction (q-PCR), fluorescence in situ hybridization (FISH), phospholipid fatty acid quantitation (PLFA), molecular fingerprinting of 16S rRNA gene fragments including denaturing gradient gel electrophoresis (DGGE) and terminal restriction fragment length polymorphism (TRFLP), and high-throughput sequencing (also known as next-generation sequencing, or NGS) of soil microbial genes (Chen et al., 2013; Hale et al., 2014; Kolton et al., 2011; Mackie et al., 2015; Rousk et al., 2009). Changes in the relative abundances of Acidobacteria, Actinobacteria, Gemmatimonadetes, and Verrucomicrobia are frequently detected using high-throughput sequencing, under treatment with biochar (Mackie et al., 2015; Nielsen et al., 2014). With higher resolution to the species level, the metagenomics sequencing of microbial genes is able to realize function annotation reflected by the soil microbial community structure changes (Jäckel et al., 2004). Such a process is essential to explain the effects of biochar on soil remediation (Chen et al., 2013; Hale et al., 2014; Kolton et al., 2011; Mackie et al., 2015; Rousk et al., 2009). Since the mechanisms underlying biochar's effects on microbes and related soil functions and processes are still not quite clear, this review focuses on the synthesis of several possible mechanisms based on the published research.

The influences of biochar on microbial activity are diverse and seven possible mechanisms are demonstrated in the central circle of Fig. 1 (from which points 1 to 3 can be classified into direct influences, and points 4 to 7 indirect influences): (1) biochar provides shelter for soil microbes with pore structures and surfaces (Quilliam et al., 2013a); (2) biochar supplies nutrients to soil microbes for their growth with those nutrients and ions adsorbed on biochar particles (Joseph et al., 2013); (3) biochar triggers potential toxicity with VOCs and environmentally persistent free radicals (Fang et al., 2014a); (4) biochar modifies microbial habitats by improving soil properties that are essential for microbial growth (including aeration conditions, water content, and pH) (Quilliam et al., 2013a); (5) biochar induces changes in enzyme activities that affect soil elemental cycles related to microbes (Lehmann et al., 2011; Yang et al., 2016b); (6) biochar interrupts microbial intra- and inter-specific communication between microbial cells via a combination of sorption and the hydrolysis of signaling molecules (Gao et al., 2016; Masiello et al., 2013); it should be noted that biochar may contain some molecules that can work as signals for microbial communication; and (7) biochar enhances the sorption and degradation of soil contaminants and reduces their bioavailability and toxicity to microbes (Beesley et al., 2010; Qin et al., 2013; Stefaniuk and Oleszczuk, 2016). The proposed mechanisms involved in biochar-microbe interactions need further experimental verification, and a research emphasis should be placed on the linkage between biochar-microbe interaction mechanisms and their environmental effects.

2.1. Biochar provides shelter for microbes

One hypothesis of the benefits of biochar for microorganisms is that biochars can be shelters for microbes due to their pore structures. Biochars provide more habitable pore volume per unit volume than soil does (Quilliam et al., 2013a). Microbial living cells can attach on biochar surfaces; in such cases, biochars with large specific surface areas can provide habitats for microbes as well (Abit et al., 2012). However, the colonization of bacterial cells and fungal hyphae has spatial heterogeneity between the external and internal pores of biochar (Quilliam et al., 2013a). Different microbial colonization patterns on the surfaces and in the pores of biochar can be explained by three phenomena: 1) there is less nutrient accessibility in biochar pores than in natural soil pores, 2) the biochar pores can be blocked with soil organic matter (e.g., humic