Microbial Inoculants for Improving Carbon Sequestration in Agroecosystems to Mitigate Climate Change

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Abstract

The impacts of losing carbon from the terrestrial pool into the atmosphere have major consequences that affect many aspects of our planet in the long term and the short term. Agricultural lands could contribute in targeting these issues and provide efficient solutions, such as decreasing the level of atmospheric carbon while increasing carbon levels in soil. The proper selection of suitable microbial inoculants that are able to sequester carbon into soils is very important in order to improve agricultural land's capability to sequester and store carbon. By achieving that, soil quality and properties would increase, and atmospheric carbon would be mitigated. In this review, we discussed the potential of using microorganisms as microbial inoculants to overcome the negative impacts of losing carbon from soils, by increasing carbon levels in soils. Soil microorganisms have the ability to affect the organic matter quantity and quality, which leads to affecting soil ecology and properties. Fungi and bacteria contribute differently in soil carbon sequestration by regulating multiple and different pathways inputs and losses of soil carbon such as possessing metabolic activities that can capture CO_2, the ability to sediment carbonates, the recalcitrant nature of their vegetative and products tissues, or the formation of stable forms that protect carbon in soil. More studies are needed to test the potential of certain microbial strains with carbon sequestration ability to improve soil quality and mitigate climate change.

Keywords

Agroecosystems · Bacteria · Carbon sequestration · Climate change · Fungi · Microbial inoculants · Global warming · Soil fertility · Soil health

Introduction

Soil is considered the largest carbon reservoir, as it contains more carbon than the atmosphere and vegetation combined (Averill et al. 2014; Tan et al. 2014). Soil organic matter is composed of organic fractions that contain decomposed animals and plants as well as microbial organisms, in addition to inorganic forms such as carbonates and lime (Chan 2008). Two types of components present in soil organic matter are active (35%) and passive (65%), in which active soil organic matter is living organisms as well as dead animals and plant residues that contain easily digested sugars and proteins; meanwhile passive soil organic matter is the components present in the soil that are hard to decompose by microbes (Hoorman and Islam 2010). All these different types of soil components affect soil ecology and properties.

Soil organic carbon originally comes from atmospheric CO_2 that is captured via a process called photosynthesis by plants and autotrophic organisms to turn atmospheric CO_2 into organic compounds (such as sugars and cellulose) which build up their biomass. The rate of atmospheric CO_2 that is captured through photosynthesis and enters terrestrial biomass is about 120 Pg carbon per year, half

of which will be lost again from plants to the atmosphere by respiration, and the net production will be about 60 Pg per year (Fig. 1) (Amundson 2001; Janzen 2004). This amount will stay in a form of temporarily vegetative tissues. Afterward, other living organisms will feed on the plants, build up their biomass from carbon compounds, and then release some of the carbon as CO_2 to the atmosphere through respiration. After organisms die and decompose (e.g., plants and animals), carbon in the organic matter will return into the soil where it might stay until being broken down by soil microorganisms and released back to the atmosphere in the form of CO_2. Heterotrophic respiration, which is largely done by microorganisms in soil, and fire return an amount of carbon estimated to be ~60 Pg carbon per year back to the atmosphere in the form of CO_2 (Fig. 1) (Janzen 2004).

Soil contains about 2344–2500 Gt of carbon, of which about 1550 Gt of carbon is stored in organic forms and 950 Gt stored in inorganic forms (Fig. 1) (Lal 2004; Stockmann et al. 2013). There is a constant need to reduce carbon emissions and remove carbon from the atmosphere in order to fight against climate change and to overcome the negative impacts of losing carbon from the terrestrial pool to the atmosphere. High concentrations of atmospheric CO_2 ($\geq$400 ppm) lead to an increase in temperatures of more than 2–4 °C, causing changes in wet/dry cycles, heavy and intensive rainfall and storms, extreme frost and heat waves, and increased fire frequency. It also significantly influences environmental quality and water resources, crucially affects soil fertility and properties, and significantly abrupts changes in temperatures daily, seasonally, and interannually (Qafoku 2015). Due

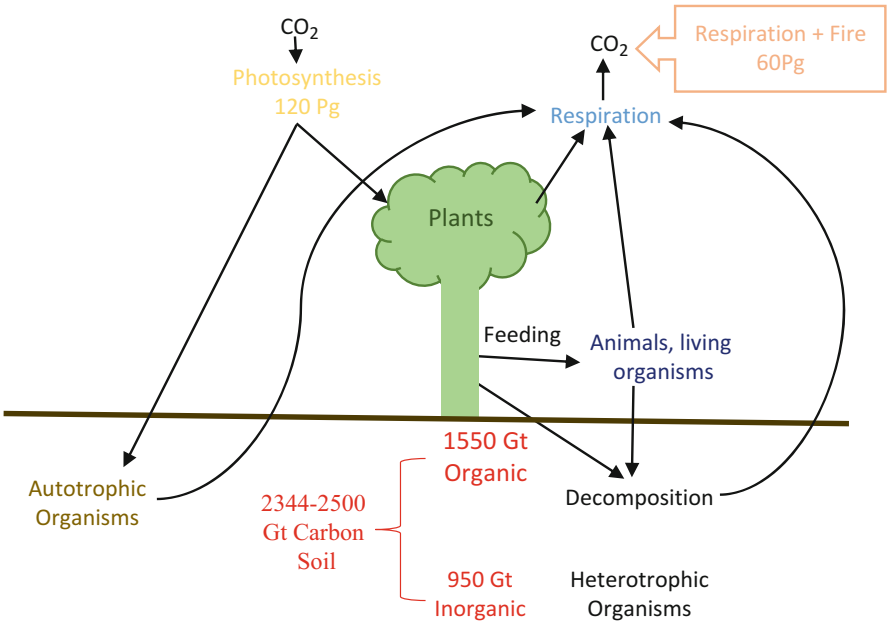

Fig. 1 Carbon sequestration and cycle in terrestrial ecosystems

to these negative effects that are mainly caused by the large losses of soil carbon to the atmosphere, intensive studies should be undertaken to decrease carbon losses from soils as well as reduce atmospheric CO_2 levels.

The Impact of Losing Carbon from Soils on Agricultural and Climatic Conditions

Agricultural Conditions

Soil organic matter contributes significantly to soil's quality and fertility (Chan 2008), and it contains an amount of 58% of soil organic carbon (Stockmann et al. 2013). Thus, losing carbon from the soil will affect the soil's conditions and properties, which directly influence agricultural production. Soil organic matter increases the availability of nutrients in the soil through the decomposition of the organic matter, which will release phosphorus, nitrogen, and other important nutrients for plant health and growth (Chan 2008). Enough amount of organic matter in soil will ensure the availability of all nutrients that are important for plant health and growth. Losing organic matter from soils leads to decreasing the efficient amount of these nutrients, which would affect plant growth and health and directly leads to decreased plant productivity.

Soil organic matter enhances soil structure and physical properties such as water filtration, water-holding capacity, root growth, gaseous exchange, and ease of cultivation through soil aggregation formation (Chan 2008). Suitable soil structure and physical properties directly affect soil quality leading to better soil conditions. These conditions will contribute to optimize the soil ecology to provide all the required factors for plant's growth. Thus, losing or decreasing the organic matter in soil will disrupt these optimal conditions through disrupting the soil structure and physical properties, which will then affect plants. Soil organic matter significantly contributes in decreasing soil loss and runoff as well as reducing carbon leaching; therefore it will enhance carbon sequestration in soil (Kadlec et al. 2012). Hence, soil organic matter plays a major role in improving soil properties, either directly by immediate effect or indirectly through enhancing carbon sequestering into soil that would eventually affect soil properties. Improving soil structure and physical properties is critical for creating suitable soil ecological conditions for plant growth, health, and production.

Organic matter promotes soil biological health as it is considered an important food source for soil flora and fauna. It controls the type and number of soil inhabitants and thus contributes to other important soil functions such as nutrient availability and cycling, plant nutrient uptake, root growth, burrows creation, and suppression of crop diseases (Chan 2008). Sufficient organic matter in soil contributes to enhancing different soil biological activities of useful soil microbial organisms. The reduction of soil organic matter would influence the soil microbial organisms negatively, which would affect these critical soil biological activities and plant health. Therefore, efficient amount of organic matter in soil regulates

various biological processes that contribute to nutrient cycling, as well as improving plant health and overcoming diseases.

Climatic Conditions

The loss of carbon from soils increases CO_2 levels in the atmosphere and leads to increasing global temperatures and causes global warming. Previous studies have focused on reducing carbon emissions in order to fight against climate change (Powlson et al. 2011; Shindell et al. 2012). Global temperature is reported to increase more than 2 °C by 2050 and about 3–5 °C in the coming 50–100 years (Ipcc 2007; Randers 2012). The increase in temperature correlates with the increase of the frequency of other environmental stresses such as heat waves, flood, and drought (Trenberth 2011; Jansen et al. 2014). These environmental stresses will affect agricultural lands afterward.

Drought affects plants by causing water stress in them, which could negatively affect their growth and health. Water is a necessity for plants. Therefore, the lack of water availability will damage plants by affecting important biological processes such as photosynthesis (Ghotbi-Ravandi et al. 2014) and then affect metabolisms and reduce plant growth and health.

Plant biochemical reactions are highly sensitive to high temperatures, and high temperature stress leads to affecting plants' metabolism, growth, and productivity (Hasanuzzaman et al. 2013). Strong impacts on plants are caused by heat waves through decreasing growth as well as shifting biomass allocation, and when heat waves combine with drought, it could be devastating for plants and lead to mortality (Teskey et al. 2014). Heat waves put plant under heat stress. This influences plants by affecting important biochemical reactions that are necessary for plant growth and health, which would limit plant yields. The continuous increasing of global temperature would contribute in decreasing the production of agricultural lands.

Flooding could affect agricultural production through changing the physiological and chemical properties by leaching organic matter and nutrients down the soils (Eni et al. 2011). Plants need adequate moisture in the soil to ensure optimized crop yields, and the decrease or increase of these levels will directly affect plant health and growth and will affect crop production eventually. The increase in global temperature could also affect agricultural lands through reducing the cultivated areas. The increase of temperature will melt the tundra, and then oceans would expand and decrease agricultural lands. It is predicted that ocean expansion in the next 40 years will cause sea level to raise 30 cm (Randers 2012). Thus, agricultural lands could face considerable reduction in size that definitely decreases agricultural production.

High temperatures could provide suitable conditions for pathogens growth and spread (Luck et al. 2011). In extreme weather, certain plant diseases such as powdery mildews and rusts could be sporadic and develop more quickly in warm conditions (West et al. 2015). Thus, controlling global temperature through sequestering carbon

and reducing CO_2 mitigation could participate in controlling plant diseases subsequently. Maintaining plant health by controlling and limiting plants susceptibility for diseases would positively enhance crop yields and quality. Therefore, we reviewed the use of microbial inoculants as means to significantly enhance carbon sequestration in the soil, thereby mitigating against climate change.

Soil Carbon Sequestration

Carbon sequestration is a term used to describe a process that leads to increase soil organic carbon storage by removing CO_2 from the atmosphere and introducing it into soils. It is defined as the process of transferring atmospheric CO_2 into the soil of a land unit through unit plants, plant residues, and other organic solids in order to be retained in the unit as part of the soil organic matter (Olson 2013). Carbon could be stored in soils as stable long-lived forms of organic matter (Six et al. 2006; Powlson et al. 2011). Increasing the concentrations of hard-to-decompose organic forms in soil will lead to securely stored carbon in soils for long periods and to reduction of carbon emissions. The balance between carbon inputs and outputs determines soil carbon sequestration and the change in soil organic carbon levels (Chan 2008). The more carbon stored in the soil and less carbon lost indicates that this land has high ability to sequester carbon, and vice versa. Soil organic carbon levels are affected by management practices such as cultivation, overgrazing, and stubble burning or removal (Chan 2008). Therefore, poor management practices will affect carbon sequestration negatively and lead to depletion of soil organic matter in soils. Carbon levels and storage in soils result from the interaction between several ecological processes, which are photosynthesis, respiration, and decomposition (Ontl and Schulte 2012). Photosynthesis (by either plants or autotrophic organism) contributes to carbon sequestration process through increasing the amount of CO_2 input from the atmosphere to the terrestrial pool. Meanwhile respiration and decomposition contribute to losing carbon from the terrestrial pool back to the atmosphere. Due to this, studies should focus more on the processes that increase carbon sequestration and input in soils and decrease the level of carbon losses and emissions. Therefore, application of microbial inoculants is very paramount in this review.

Using microbial inoculants in agricultural practices could help to achieve desirable characteristics in soil. Bio-sequestration is the process that includes the natural capture and storage of CO_2 by photosynthetic organisms as well as soil microbes (Macreadie et al. 2014). Microbial inoculants could be used to increase the level of carbon inputs and decrease the levels of carbon outputs in the soils. Soil microbial communities have important roles in carbon sequestration and soil carbon emission (Fang et al. 2014). Choosing the right microorganism with the right mechanism for a specific land is very important in order to increase carbon sequestration in soils. Changes in microbial communities affect the soil organic matter cycling and storage due to the ability of soil microorganisms to regulate multiple pathways input and loss of soil carbon (Smith et al. 2014). The difference

in microbial biomass contents and physiological characteristics between microbial communities can lead to different mechanisms and pathways in sequestering carbon into soils.

Microbial Inoculation in Agricultural Soils

Microbial inoculation can be defined as the application of cost-effective and eco-friendly formulated microbial inoculants that can be used as renewable plant nutrient sources and can be considered an alternative method to chemical pesticides and fertilizers (Babalola and Glick 2012; Selvakumar et al. 2012). This environmentally friendly approach plays a major role in maintaining sustainable agriculture by acting as natural biopesticides and bio-fertilizers, which reduce the negative effect of using mineral fertilizers and chemical pesticides on agricultural lands as well as agricultural crops, that might lead to environmental and health consequences.

Microbial inoculants provide agricultural soils with suitable conditions that ensure high protection and yield of crops. Agricultural lands with poor chemical and physical soil properties, under stressed or normal conditions, and with low soil organic matter, lead to a reduction in crop yield and quality. In poor lands, crop yield and quality were dramatically increased after using microbial inoculants (Tavasolee et al. 2011; Upadhyay et al. 2011; Wu et al. 2014a, b). Microbial inoculants increase the level of organic carbon, nitrogen, potassium, and soil respiration (Sangakkara et al. 2014); thus they could be used as an effective solution to restore soil quality and fertility in poor lands.

Microbial inoculants are very important in agricultural systems for many benefits that they can provide, such as promoting plant growth (Bashan et al. 2014), reducing heavy metals toxicity (Sessitsch et al. 2013; Wani and Khan 2013), enhancing drought tolerance of plants (Ortiz et al. 2015), alleviating plant growth stresses (Miransari 2010), protecting against different types of pathogens (Babalola 2010), and enhancing nutrient uptake (Mardukhi et al. 2011). In addition, microbial inoculants are considered by Pal and Pandey (2014) the key determination factor of soil quality. For all these benefits, microbial inoculants could be the best solution for improving agricultural lands and to solve unfavorable soil conditions that lead to directly and/or indirectly affect crop yield and quality.

Microbial Inoculants and Carbon Sequestration

Soil microorganisms contribute to carbon sequestration by different mechanisms such as possessing metabolic activities that capture atmospheric CO_2, the ability to sediment carbonates, forming recalcitrant vegetative tissues and products, and the ability to form stable forms such as soil aggregates that protect carbon soil organic forms. Total microbial biomass in soil is composed of 0.1–2% active, 42% dormant, and 56% dead microorganisms (Blagodatskaya and Kuzyakov 2013). Microorganisms contribute to soil physical characteristics and chemical contents

through their living state as well as dead and dormant states. Different microbial communities vary in their metabolic activity states, which would lead to different effects on soil organic matter quantity and quality. The mycorrhizal and rhizobacterial type affects soil carbon independently and far more than the effects of soil clay contents, precipitation, temperature, and net primary production (Averill et al. 2014). Therefore, it is very important to study the possibility of using a specific microbial strain as microbial inoculant in order to sequester carbon in agricultural lands.

Bacterial Inoculants and Carbon Sequestration

Bacteria exist in large numbers in soil compared to fungi. Although previous reports had already discussed the ability of fungi to contribute more than bacteria in carbon sequestration (Six et al. 2006; Li et al. 2015), some reports showed that some bacterial strains have the ability to reduce CO_2 and could contribute to carbon sequestration and to mitigate atmospheric CO_2 levels (Han et al. 2013; Komala and Khun 2014; Nie et al. 2015). This indicates that bacteria could contribute to carbon sequestration through different pathways and metabolic activities.

Pseudomonas fluorescens is a plant growth-promoting bacterium that could be a useful tool for carbon sequestration and climate change mitigating (Nie et al. 2015). The results from this study indicate that this microbial inoculant increased plant productivity as well as having potential to mitigate high atmospheric CO_2 levels by increasing terrestrial carbon sequestration, particularly in high-CO_2 ecosystems. These findings could draw attention to the use of plant growth-promoting bacteria as microbial inoculants to sequester atmospheric CO_2.

Carbonate induction by some bacteria has the potential to capture atmospheric CO_2 and sequester carbon (Peng et al. 2010). *Bacillus mucilaginosus* produces carbonic anhydrase that first captures the atmospheric CO_2 and then fixes the atmospheric CO_2 through bacterial metabolism (Zhang et al. 2011). This process induces carbonate formation to form organic substances or carbonated minerals by fixing CO_2 from the atmosphere, which leads to decreased CO_2 levels and increased carbon sequestering in soils. In a recent study conducted by Xiao et al. (2015), further work was done to transcribe and translate carbonic anhydrase genes from *Bacillus mucilaginosus* genome into *Escherichia coli* to test the ability of this type of carbonic anhydrase to promote $CaCO_3$ precipitations. Results showed that the engineered bacteria produced carbonic anhydrase that helps in $CaCO_3$ formation in a relatively short time. In this regard, microbial strains that are able to produce carbonic anhydrase could be very useful microbial inoculants in the process of carbon sequestration and capturing atmospheric CO_2.

Bacterial strains with the ability to sediment carbonates such as *Bacillus pumilus* (Komala and Khun 2014), *Bacillus cereus* (Han et al. 2013), *Bacillus mucilaginosus* (Zhang et al. 2011), and *Bacillus pasteurii* (Stocks-Fischer et al. 1999) were reported to reduce CO_2 and could contribute to the carbon cycle and sequestration. These strains with other soil microorganisms that have the same ability could further

be explored for use as microbial inoculants potential to sequester carbon in soils. The sequestration of CO_2 into sediment carbonates by bacteria could be a promising option in the quest to find solutions for increasing soil carbon sequestration and reducing carbon emissions.

Chen et al. (2012) genetically engineered *Synechococcus elongatus* PCC 7942 cyanobacteria to combine the biological CO_2 fixation with the chemical transformation of CO_2. This review also introduces the insight that CO_2 bio-mitigation could be enhanced through genetic engineering by CO_2 capturing or transformation via carbonic anhydrase, with biological fixation of the captured CO_2 to participate in biomass generation. Microorganisms could be genetically engineered to overcome low efficiency of CO_2 capturing and fixation. Then, these microbes could be further studied for their ability to be used as microbial inoculants for carbon sequestration in agricultural lands.

Fungal Inoculants and Carbon Sequestration

Fungi exist in a smaller population than bacteria, but they dominate the soil biomass, especially when soil is not disturbed (Hoorman et al. 2009). Fungi contribute more than bacteria to carbon sequestration and organic matter formation and stabilization in soil (Six et al. 2006; Li et al. 2015). This is due to that fungal tissues input large amount of carbon into soil and lead to the integration of more carbon into soil fungal biomass, having recalcitrant biomass tissues and by-products, and enhance carbon protection and stabilization by soil aggregate formation.

Effects of Fungal Mycelia on Carbon Sequestration

Fungi contribute to carbon accumulation and losses in soil through fungal biomass and by-products production as well as fungal necromass degradation. Carbon accumulation by fungi in soil varies according to difference between fungal species and fungal biomass content (Fernandez and Koide 2011; Ekblad et al. 2013). Fungal mycelium is one of the vegetative tissues which grow and spread into soils in order to provide the fungi with the required water and nutrients. The production of extrametrical mycelium could reach hundreds of kilograms per ha per year (Wallander et al. 2013). Since fungal mycelium is built up by carbon, the more fungal mycelia produced, the more carbon is captured in the soil. Therefore, fungal mycelia could be considered as a vital carbon sink to the soils.

Fungal necromass is the main microbial source of stable soil organic matter and contributes more than bacterial necromass (70.7% vs. 25.9%) to soil organic matter (Li et al. 2015). Thus, mycelial necromass could be a very important source of carbon storage in soil; and it could be an important source of carbon for living organisms as well. High chitin and nitrogen concentrations in fungal mycelium would contribute to the decomposition of mycelial necromass within weeks; meanwhile melanized cell wall mycelium is resistant to decomposition, which leads to long-term preservation of necromass in soil according to the concentration level of melanin in fungal tissues (Fernandez and Koide 2011; Drigo et al. 2012; Fernandez

and Koide 2014; Koide et al. 2014). The ability of mycelial necromass to resist decomposition varies according to fungal species and the composition of fungal tissues. Thus, some fungal species could contribute to sequestering carbon more than others could. Fungal mycelia could grow into secure soil forms such as soil aggregates (Peng et al. 2013). Moreover, fungal necromass will remain protected from degradation for a long time. The more fungal necromass remains protected, the more carbon will be kept secured in soils.

Effects of Fungal Metabolites (Glomalin) on Carbon Sequestration

Glomalin is an insoluble hydrophobic glue-like proteinaceous substance (Peng et al. 2013), which is released from spore and hyphae of mycorrhizal fungi and *Scutellospora*, *Acaulospora*, *Entrophospora*, *Glomus*, and *Gigaspora* genera in order to protect the hyphae from drying out (Singh 2012; Pal and Pandey 2014). Glomalin affects carbon sequestration through two ways. First, the production of glomalin assists the formation of soil aggregates, which subsequently will affect carbon sequestration. The second way is due to the recalcitrant nature of glomalin, which makes it hard to decay, and it thus remains stable in soils for long periods.

Wu et al. (2014a, b) tested direct and indirect effects of different factors such as roots, mycorrhizal hyphae, and glomalin on aggregate stability and found that glomalin-related soil protein was the primary contributor to aggregate stability among all tested factors. This indicates that glomalin is the main factor that influences the carbon sequestration and storage in soil, either directly or indirectly by influencing other carbon sequestration factors. Glomalin attaches to soil particles and organic matter to form clumps. These clumps are stable structures that resist outside factors such as erosion, and at the same time, it has permeable characteristics that allow air, roots, and water to move inside these clumps. Soil particles and other organic and inorganic materials inside these clumps will remain protected for a long time, and this would increase the level of carbon in soils, which provides soil with good characteristics and gives soil better texture.

Since glomalin contains carbon and is abundant in soils, it could account for a considerable amount of the terrestrial carbon pool. Glomalin does not easily dissolve in water, and it resists microbial decomposition and could remain in soil for long periods, about 10–50 years (Wright and Upadhyaya 1999; Pal and Pandey 2014). The recalcitrance and complex nature of glomalin contribute significantly to carbon sequestration and storage in soil.

Effects of Soil Aggregation on Carbon Sequestration

Soil aggregation is a process that depends on providing glue-like materials by microorganisms to hold soil particles and other organic and inorganic materials together to form soil aggregates. Soil fauna and microorganisms, roots, environmental variables, and binding factors (such as glomalin) are the major factors that play a role in the formation and stabilization of aggregates (Pal and Pandey 2014). Root and fungal hyphae are considered the most important biotic factors in stabilization of soil aggregates (Singh et al. 2013). The soil aggregates form when fungal hyphae

encircle soil particles and other solid materials, while glomalin acts as a gluing agent to stick particles together to form stable structured clumps, which are called aggregates. The cementing capacity of soil aggregates provides a stable uniform structure, which protects the organic and inorganic materials that are contained inside the soil aggregate. Stabilization of aggregates contributes to carbon sequestration through protecting carbonaceous compounds inside the aggregates from degradation, which keeps carbon stored and sequestered in soils for long periods.

Soil aggregates are important to maintain and improve soil fertility, especially when targeting soil physical properties (Rawlins et al. 2013; Pal and Pandey 2014). The soil aggregates help to overcome the unfavorable conditions of soils such as looseness, runoff, leaching and erosion. At the same time, soil aggregates increase other favorable conditions such as soil structure stability, nutrient supply capability, water-holding capacity, porosity, and aeration. These useful effects can work in concert to improve soil quality and fertility. The abundance and stability of soil aggregates are very important contributors in soil quality, as well as being critical for several properties of soils.

Method Used to Determine the Effects of Microbial Inoculants in Improving Carbon Sequestration, Soil Fertility, and Climate Mitigation

For nearly a century, soil organic matter (SOM) formation in conceptual and quantitative models has been depicted primarily as a function of plant inputs and their chemistry (Waksman 1936; Berg and McClaugherty 2003; Lehmann and Kleber 2015). As such, chemically diverse and stable SOM originates from the preservation of biochemically recalcitrant complex plant polymers, such as lignin derivatives and long-chain lipids (Waksman 1936; Berg and McClaugherty 2003). However, soil microbial communities are adept at decomposing a wide range of plant compounds and using the carbon (C) to synthesize their own biomass. The importance of soil microbes in processing plant inputs and synthesizing SOM is very paramount, because formation and stabilization of SOM is a great tool to determining how carbon is being controlled, level of soil fertility, and climate mitigation. Therefore, this review discussed the use of model soils to quantitatively assess whether microbial processing of simple C (i.e., low-molecular-weight) substrates alone, in the absence of complex plant compounds, can build significant amounts of chemically diverse, stable SOM. Since this model soils are initially C- and microbe-free, we eliminate the difficulties of isolating microbial residues that occur when using natural soils. We use a gradient of substrate-C inputs to represent different microbial-available energy in order to facilitate the development of diverging microbial communities and physiologies that are hypothesized to influence SOM chemistry and accumulation rates. The substrate gradient includes monomeric and dimeric sugars since they are abundant energy sources for microbial metabolism in natural soils (Fischer et al. 2010), but also because their rapid microbial uptake and intercellular breakdown should leave little to no unaltered substrate in the soil

that would interfere with the detection of novel SOM molecules formed during the experiment (Baldock et al. 1989; Fischer et al. 2010). Further, we include a more recalcitrant lignin monomeric substrate, as well as plant-derived dissolved organic C (DOC), a natural analog to test whether substrate chemical diversity is requisite to generating SOM chemical diversity. We also compare two clay types (kaolinite or montmorillonite) to investigate the effects of clay mineralogy on SOM accumulation relative to microbial communities and substrate chemistry. We characterize the composition of SOM after 18 months of incubation using high-resolution molecular fingerprinting by pyrolysis-gas chromatography/mass spectrometry (py-GC/MS) to establish the chemical fingerprint of newly formed microbial residues (including cell wall and cytoplasmic materials, metabolites, and extracellular excretions). Our model soils accrue C concentrations between 1 and 1.4% C, with a chemical diversity and stability characteristic of natural soils. Substrate type has a stronger influence on SOM development than clay mineralogy. However, this effect appears to be an indirect consequence of diverging microbial communities, where different substrates select for distinct microbial communities, with microbial-SOM accumulation being greatest in soils where microbial abundances are highest and microbial biomass production is most efficient.

Method

Experimental Conditions and Sampling

Laboratory mesocosms consisted of 100 g dry wt of 33% kaolinite or montmorillonite clay mixed with quartz sand. The cation exchange capacity was 5.2 and 28.6 mg per 100 g soil for the kaolinite and the montmorillonite soil mixtures, respectively. Metal concentrations for the kaolinite mixture were 5.6% Al, 1% K, 0.9% Fe, 0.14% Ca, 0.11% Na, and 0.06% Mg. Montmorillonite mixture metal concentrations were 2.2% Al, 0.8% K, 2.3% Fe, 0.39% Ca, 0.14% Na, and 0.32% Mg. Soil mixtures received weekly additions of glucose, cellobiose, syringol, or switchgrass plant DOC (0.7 mg C per g dry soil) and biweekly additions of a multi-nutrient Hoagland's solution (0.023 mg N per g dry soil). The substrate-C (5 ml of 14,000 ppm C) and nutrient additions (0.5 ml of 4666 ppm N) were syringe-injected throughout the model soils to facilitate uniform substrate application. The rate of weekly C additions reflects the upper range of natural C inputs to soil from daily root exudations. Total C inputs from added substrates over the course of 15 months amounted to 46.9 mg C per g soil, and total inorganic N from nutrient solution was 1.56 mg N per g soil. To create DOC, we mixed 150 g switchgrass (*Panicum virgatum*) tissue (leaf, stem, and seed) with 2 l H_2O and shook for 24 h before filtering. The filtrate was then partially evaporated until the C concentration was 18 mg C per ml (C:N 20). We created the microbial soil inoculum in a soil slurry (1:100 w/v) using soil collected from a Michigan bromegrass (*Bromus inermis*) field at 0–7 cm depth. We then syringe-injected 100 µl of inoculum solution (~0.00001 g natural soil per g model soil) into the soil mixture. Each soil mesocosm treatment was replicated five times with five destructive harvests at 6, 9, 12, 15, and 18 months.

During incubation, soils were maintained at 25 °C, 45% water-holding capacity, and a pH between 4.6 and 5. The pH of DOC-treated soils, however, increased to 7 after a few months of incubation, and therefore DOC biological data are minimally included in our analyses. During the 15-month incubation period, no soil mixing occurred in order to better simulate an undisturbed soil environment and to minimize aggregate destruction.

After 15 months, substrate and nutrient additions ceased, but soils were maintained for an additional 3 months under the previous incubation conditions with periodic hand mixing to facilitate microbial uptake of any remaining substrate or unstabilized microbial biomass. Microbial community activity was monitored weekly by CO_2 flux measurements for the first 9 months and then biweekly thereafter and by microbial hydrolytic and oxidative potential enzyme activities (Saiya-Cork et al. 2002) at each mesocosm harvest.

SOM Chemistry and Concentrations

SOM chemistry was assessed using pyrolysis-GC/MS (Grandy et al. 2009). Compound peaks were analyzed and identified with the Automated Mass Spectral Deconvolution and Identification Systems (AMDIS V 2.65) software and the National Institute of Standards and Technology (NIST) compound library and published literature (Grandy et al. 2009). Organic matter compounds are expressed as the % relative abundance of total sample peak area and classified based on origin (lipids, lignin derivatives, polysaccharides, proteins, nonprotein N-bearing, and phenolics). Identifiable compounds with potentially multiple origins were classified as unspecified. Aromatic compounds also with an unspecified origin were classified as aromatics. The SOM chemical diversity was determined based on the total number of identifiable compounds that were >1% relative abundance.

Total SOC concentrations were determined on an elemental analyzer (Costech ECS 4010). Total microbial biomass carbon (MBC) was determined by the difference in C concentration (using a Shimadzu TOC-L analyzer) in chloroform fumigated and unfumigated soil subsamples extracted with 0.5 M K_2SO_4. We calculated the total SOM conversion efficiency as the amount of total SOC relative to the total substrate-C added for each destructible harvest, where the total substrate added is the sum of the weekly substrate addition within the time period up until harvest.

SOM Stability

Determination of biological stability was performed in a separate 3-month incubation on soil subsamples harvested at 6 months. During this separate incubation experiment, soils received three applications of ^{13}C-labeled 1:1 glutamic acid/glucose 25 atom % mixture at 50 μg C per g soil. The labeled substrate enabled us to use a standard isotope mixing model (Ineson et al. 1995), to determine the amount of newly formed C vulnerable to decomposition by an active microbial community. During the 3-month incubation, soils were frequently hand-mixed to facilitate SOM mineralization and maintained under the same incubation conditions as the long-term incubation. We also assessed the chemical stability of the accumulated SOM with acid hydrolysis fractionation (Paul et al. 2001). After the full 18-month

incubation, 1 g soil was treated with 50 ml 6 M HCl and heated at 100 °C for 18 h. After heating, the acid hydrolysable fraction was decanted, and the remaining nonacid hydrolysable (i.e., stable) residue was rinsed four times with DI-H_2O and isolated by centrifugation (Paul et al. 2001; Plante et al. 2011). The chemically stable C was then determined based on the differences in C remaining in the nonacid hydrolysable residues and the initial C content of the sample.

Microbial Community Composition

Determination of differences in microbial community composition was performed from PLFA biomarkers, identified and quantified at 12 and 15 months (Guckert et al. 1985). We included a phosphate buffer in the single-phase solvent system (chloroform) to extract only viable microorganisms. Lipid extracts were fractionated on silicic acid columns to isolate and collect polar lipids. Polar lipids were methylated to fatty acid methyl esters with 0.2 M methanolic KOH, purified and then analyzed on a Varian 3800 GC-FID. Peaks were quantified using internal standards, and identification was based on retention time data with known standards. Fungal relative abundance was determined by the sum of polyenoic unsaturated fatty acids (18:2ω6 and 18:1ω9c); Gram-positive relative abundances by the sum of the total branched, saturated fatty acids (i15:0, a15:0, i16:0, i17:0, and a17:0); and Gram-negative relative abundances by the sum of monoenoic and cyclopropane unsaturated fatty acids (16:1ω7c, 16:1ω7t, cy17:0, 18:1ω7c, and cy19:0). We did not detect any actinobacterial fatty acids.

Soil Microbial CUE and Enzyme Activities

Characterization of microbial CUE at 9 and 15 months was carried out by measuring the amount of a ^{13}C-labeled glutamic acid incorporated into MBC and respired as $^{13}CO_2$–C (Frey et al. 2013; Kallenbach et al. 2015). Fresh soil subsamples were amended with 25 atom% labeled ^{13}C-glutamic acid (50 μg C per g dry soil, <1% total soil C) and incubated at 25 °C for 22 h. The 22-h incubation time was based on preliminary respiration curves to determine the period when the majority of glutamic acid is utilized but before substrate recycling begins. Following incubation, soils were extracted for ^{13}C-glutamic acid incorporation into MBC by extracting and analyzing MBC as discussed previously and determining its isotopic composition on a 1030 TOC Analyzer (OI Analytical, College Station, TX) interfaced with a PDZ Europa 20–20 isotope ratio mass spectrometer. A 12-ml CO_2 sample was also collected for determining $^{13}CO_2$–C respiration on a GC-isotope ratio mass spectrometer (Thermo Scientific, Bremen, DE).

This approach estimates the amount of C allocated to biomass per unit of C substrate consumed and represents a proxy for microbial CUE. We calculated CUE

as [$MB^{13}C/(MB^{13}C + {}^{13}CO_2–C) \times 100$], where $MB^{13}C$ and $^{13}CO_2–C$ were determined using a standard isotope mixing model equation (Bradford et al. 2013) and represent the amount of substrate incorporated into MBC and the substrate-C respired as CO_2, respectively. We used glutamic acid to estimate microbial community CUE across all substrate-treated soils since it is taken up directly into microbial cells. This approach allows us to more directly compare CUEs across treatments since substrate-C allocation toward enzyme production is minimized and we can better approximate the efficiency of new biomass growth rather than substrate degradation efficiency (Geyer et al. 2016).

The potential activities of microbial extracellular enzymes were measured at 6, 9, 12, and 15 months of incubation. We used a standard fluorometric method to assess hydrolytic enzyme activity by adding 1 g soil dry weight homogenized in a slurry with 50 mM sodium acetate buffer (Saiya-Cork et al. 2002). The buffer solution was adjusted to the average soil pH of 4.9. Soil homogenates were added to black, 96-well microplates with compound-specific fluorescing substrates bound to methylumbelliferone. Oxidative enzyme activity (phenol oxidase and peroxidase), associated with lignin breakdown, was measured spectrophotometrically using clear 96-well microplates.

Statistical and Data Analyses

Data were analyzed using a linear mixed-model two-way analysis of variance (ANOVA) to determine differences in SOM chemistry, SOC concentration, SOC conversion efficiency, SOC stability, and PLFAs and CUE between clay mineralogy and substrate type. Treatment replicate ($n = 5$) was used as a random effect, and clay and substrate were treated as fixed effects. Since the experimental design was unbalanced (there was no syringol treatment within kaolinite soils), analyses for differences in main effects of substrate and mineralogy and their interactions did not include syringol. A one-way ANOVA was used to examine the effect of substrate within a clay treatment, allowing us to include syringol-treated soils in our comparisons. In many analyses the glucose and cellobiose treatments were not statistically different ($P > 0.05$). In these cases, glucose and cellobiose data were averaged and reported as a "sugar" treatment. Pair-wise comparisons between treatments were determined by Tukey's HSD ($P < 0.05$). We used Pearson's correlation analysis to examine relationships between SOC concentrations, microbial CUE, microbial community composition, and SOM chemistry. All ANOVA and correlation analyses were performed in SAS v.9.3 (SAS Institute, 1999) using PROC MIXED and PROC CORR. When necessary, data were normalized using log transformation before analysis of variance analyses. Significance for all analyses was determined at a probability level of $P < 0.05$ unless otherwise stated. Variation around means is reported or shown as standard error.

We also used non-metric multidimensional scaling (NMDS) (PC-ORD; version 4.14) to explore differences in SOM chemistry and community composition. Pyrolysis-gas chromatography/mass spectrometry compound relative abundances and PLFA biomarkers were relativized to maximum and used separately in NMDS matrices. We also used NMDS to determine relevant parameters influencing SOC concentrations for use in our correlation analyses, where SOC concentrations at 9, 12, 15, and 18 months were grouped a priori into low, medium, and high SOC concentrations. The Sorensen (Bray-Curtis) index was used as a distance measure for all ordinations. Final NMDS solutions were considered acceptable if Monte Carlo simulations had stress values <20 and a solution stability of <0.005. Determination of significant groupings was done by the Monte Carlo stress reduction ($P < 0.05$) and multi-response permutation procedure ($P < 0.05$).

Carbon Sequestration and Agroecosystems

Different agricultural management practices affect carbon stocks in soils either positively or negatively. It is essential to adopt agricultural practices that maintain a sufficient level of carbon stocks with the goal of enhancing agricultural production and climate mitigation. The balance between the inputs and outputs of carbon in soil determines the change of soil organic carbon levels (Chan 2008). In agricultural lands, the key factor to maintaining and storing enough organic matter is to increase carbon storage by increasing the level of carbon inputs and decreasing the level of carbon outputs. Many agricultural management practices improve the level of organic matter and increase the carbon input in soil, such as adding crop residues, animal manure, sewage compost and sludge, or reducing soil disturbance and enhancing rotation of crops with high carbon inputs to the soils (Caporali and Marinari 2008). Such management practices maintain soil organic matter and nutrient supplies that promote soil health. Since soil organic matter is the key factor to determine soil productivity and the level of climate pollution, it is critical to maintain its levels by different and promising practices to achieve sustainable agricultural production and climate mitigation.

Carbon sequestration has gained a lot of interest because it is considered a multiple purpose strategy to use in mitigating climate change, protecting the environment, improving diversity, restoring degraded soils, and increasing land productivity (Wang et al. 2010). This process ensures the accumulation of organic carbon in soils by sequestering CO_2 from the atmosphere. Microorganisms have the ability to capture and store carbon in soils through different mechanisms and pathways. Thus, microbial inoculants could be used to increase the level of organic carbon in soils. Moreover, microbial inoculants will provide agricultural lands with the desired manipulated condition to improve yields and productions. Microbial inoculants have the ability to convert low-output agricultural lands to more productive lands. This strategy could enhance soil quality and properties through increasing organic matter, which would lead to increased agricultural yields and climate mitigation.

Conclusion

Soil carbon sequestration is a beneficial strategy that could mitigate climate change, enhance soil quality, increase carbon levels in soil, improve agricultural production, and enhance food security. Soil organic matter contributes in different factors that play major roles in soil health and plant production such as providing nutrients, improving suitable soil ecological conditions, affecting soil quality and physical properties, and regulating important biological processes. The depletion of the soil organic matter could cause serious consequences. Thus, it is critical to maintain enough levels of organic matter in order to maximize the optimal conditions for sustainable agriculture.

Microbial inoculant is one of the major agricultural practices that has been used to acquire desirable characteristics in the soil. Soil ecological conditions for crop production could be optimized by maintaining suitable levels of organic carbon in the soil. This might be achieved by introducing environmentally friendly microbial formulations with carbon sequestering ability to the soil. Different types and species of soil microorganisms could affect carbon sequestration and storage differently in soil. These mechanisms range from different pathways and metabolic activities to the recalcitrant nature of their vegetative tissues and products.

Some bacterial species have been reported to contribute in carbon sequestration and atmospheric CO_2 mitigating. Growth-promoting bacteria have been shown to have potential for carbon sequestration, and they could be studied intensively for use as microbial inoculants for increasing carbon levels in soil. Bacteria with the ability to capture atmospheric CO_2 and/or the ability to sediment carbonates are also promising option as microbial inoculants for increasing the level of soil carbon and reducing atmospheric CO_2 levels.

Fungi also have been proved to sequester more carbon into the soil even than bacteria due to their ability to form soil aggregates, having recalcitrant biomass compounds and by-products. Fungi have three major factors that have been proved to play important roles in the ability of fungi to sequester more carbon in the soil, which are fungal mycelia (living or nonliving), production of glomalin, and the ability to form soil aggregates. Due to these characteristics, fungi participate more in carbon sequestration, and organic matter formation and stabilization. Thus, fungal microbes are good candidates to be used as microbial inoculants to increase organic carbon in soils.

This review highlights the potential of soil microorganisms to be used as microbial inoculants for carbon sequestration and the importance to select and formulate the proper microbial inoculants that are able to sequester carbon in the soil. By achieving that, agricultural production would be raised by the increase of soil organic carbon in soils, which will lead to improved soil quality as well as food security. Carbon sequestration has gained a lot of attention in the past few years due to its potential to mitigate atmospheric CO_2 and fight against climate changes. However, there are not enough studies focused on using microbial inoculants as a carbon sequestering technique to increase soil fertility and mitigate climate change.

More efforts should be undertaken to use microbial inoculants as carbon sequestration strategy to mitigate climate change and enhance soil quality and fertility in order to achieve long-term food security and agricultural sustainability.

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