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# Bacterial growth efficiency varies in soils under different land management practices

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ABSTRACT

Transformations of plant-derived carbon into soil organic carbon (SOC) influences both local and global carbon cycles. Soil bacteria play a major role in SOC transformations, which are important for maintaining soil fertility and for stabilizing carbon in soil. SOC is consumed by bacteria in soil and transformed into biomass or respired to carbon dioxide. This bacterial-driven partitioning of SOC is defined as Bacterial Growth Efficiency (BGE) and it is an integral component of models that simulate carbon dynamics. We tested the variability of BGE in microbial communities from soil by measuring bacterial production (BP) and respiration (BR), the two components of BGE, in slurries of soils collected from deciduous forests and croplands at the Kellogg Biological Station Long Term Ecological Research site. BP was measured as $^{3}$H-leucine incorporation into protein and BR as oxygen consumption. The differences in BP and BR in soil under different land management practices revealed that BGE was not static but varied from 0.23 to 0.63, supporting more recent SOC models. Bacterial communities from soils of soybean monoculture cropland tended to have a higher BGE than those from deciduous forests. BGE of cropland soil microbes exhibited a large seasonal variation not observed in forest soils. Nutrient amendments on rotation cropland soil microcosms showed that BGE is sensitive to substrate availability and nutrient stoichiometry. Using a range of growth efficiency expected of terrestrial ecosystem, simulations of carbon dynamics in a forest using the DAYCENT model revealed the sensitivity of equilibrium soil carbon values to changes in growth efficiency. Decreasing the default growth efficiency of 0.45 to a growth efficiency of 0.35 reduced the active carbon fraction by 22%. This sensitivity emphasizes the importance of site-specific BGE measurements for improving the predictive capacity of SOC models, especially when investigating the effects of changes in land management practices on labile SOC transformation. The weak correlation of BP and BR in most soil tested also showed that BGE is a more valuable measurement than the common interpretation of bacterial activity based on BR.



## 1. Introduction

Soil bacteria play a central role in transformations of soil organic carbon (SOC). Inputs of organic matter, largely in the form of root exudates and plant litter, are decomposed and transformed into bacterial biomass and carbon dioxide. Bacteria also produce metabolites and extracellular enzymes involved in humification and aggregation, both of which protect SOC from further decomposition (Six et al., 2006). Bacteria continue to contribute to the stabilization of SOC even after cell death because some components of their biomass, especially proteinaceous constituents, serve as substrates for humification (Liang et al., 2010; Simpson et al., 2007). Understanding the involvement of microbes in carbon sequestration is becoming more important as evidence accumulates for biological factors having a strong influence on the formation of soil organic matter (Jiao et al., 2010; Liang and Balser, 2011; Miltner et al., 2012).

Heterotrophic bacteria in soil depend on carbon input from plants as both carbon and energy sources. Decomposition of plant-derived carbon by soil bacteria is typically quantified in terms of the amount of $CO_2$ produced during respiration (Strickland et al., 2009). However, $CO_2$ production during decomposition is only one part of the transformation process. Increased $CO_2$ production can be due to increased substrate availability, increased decomposition rate or decreased growth efficiency. Bacterial growth efficiency (BGE) is a measure of the fraction of carbon consumed that is incorporated into new biomass by bacteria (del Giorgio and Cole, 1998; Manzoni et al., 2012). It is an informative measure of the physiological state of bacteria and their capability to stabilize labile organic carbon. In

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pure culture studies, BGE is sensitive to substrate quality and availability, and can rapidly decrease at low substrate concentrations (Tempest, 1978). BGE can also be influenced by intrinsic factors of the microbial community, such as metabolic capability and maintenance energy requirement (Schmidt and Konopka, 2009).

Growth efficiency is a central parameter in models simulating SOC dynamics and to calculate microbial turnover time in soil (Cheng, 2009; Lawrence et al., 2009; Parton et al., 1988). It is used to estimate the fraction of soil carbon pool that is transformed into $CO_2$ or microbial biomass. The incorporation of growth efficiency in carbon models is required to incorporate microbially driven carbon transformation. It is increasingly acknowledged as a fundamental component in understanding soil C cycling (Sinsabaugh et al., 2013). Traditionally, growth efficiency is treated as a global parameter or a function of soil clay content (Jenkinson, 1990; Manzoni and Porporato, 2009; Parton et al., 1987). By doing so, the assumption is made that all terrestrial ecosystems simulated by the model have microbial decomposers of equal physiology and genetic capability, and are consuming similar type of substrates. Using the same fractionation factor for different pools of carbon also assumes that carbon substrates of different stability are incorporated equally into microbial biomass. The lack of information on growth efficiency in terrestrial ecosystem makes it challenging to identify suitable growth efficiency estimates or the variability for the biomes being modeled. More recently, it is suggested that growth efficiency of terrestrial ecosystems can be highly variable and this variation should be captured in SOC simulations (Frey et al., 2013; Manzoni et al., 2012; Sinsabaugh et al., 2013).

Due to the spatial heterogeneity and complex physical matrix of soil, microbial growth efficiency measurements in terrestrial ecosystems have been sparse. Comparisons across studies are challenging because different methods and assumptions have been used (Barros et al., 2008; Dijkstra et al., 2011; Herron et al., 2009; Nguyen and Guckert, 2001; Schimel, 1988). The most common method, which is to trace the fate of radiolabeled substrate, is specific to the added substrate. Growth efficiency measurements obtained from such methods represent the efficiency of members of the community that are able to transport and metabolize the particular substrate. Due to the sensitivity of growth efficiency to the type of substrate consumed, measured growth efficiency can be different when different substrates are used (Fischer et al., 2010). In addition, organic substrates available to soil microbes are heterogeneous, vary with overlying plant species and are typically not dominated by a single substrate (Meier and Bowman, 2008).

Growth efficiency in soil is typically measured for the composite microbial community. The tight interactions between bacterial and fungal community makes it challenging to study these two communities separately. Yet, it is essential to elucidate the function of bacterial and fungal communities because they respond differently in soils under different land managements (Bailey et al., 2002). Fungi are typically assumed to use resources more efficiently than bacteria, but agricultural soils with different fungal to bacterial biomass ratio were found to have similar growth efficiencies (Thiet et al., 2006). Fungal growth efficiency can also be influenced by different nutrient requirements than bacterial growth efficiency (Keiblinger et al., 2010). It is important to distinguish the role of these two groups of organisms because it will allow us to link the dynamics of the individual community to their function in soil carbon transformations (King, 2011).

Focusing on the bacterial community, we tested the assumption that BGE is static for soils under different land managements. Bacterial production and respiration were measured using a method that is less discriminative of substrate consumed, to calculate the growth efficiency of bacterial community in slurries of soil collected from a forest and three different croplands. The sensitivity of BGE to substrate availability was determined by lab incubation of tilled, corn/soybean/wheat rotation cropland soil with different nutrient amendments. Additionally, growth efficiency in the DAYCENT model was varied to ascertain the impact of changes in growth efficiency on simulated soil organic carbon for a mock ecosystem.

## 2. Materials and methods

### 2.1. Soil samples

Soil samples were collected from the W. K. Kellogg Biological Station Long Term Ecological Research site (KBS LTER, Hickory Corners, MI) in 2010. Descriptions of the site and soil types are available at http://kbs.msu.edu. Five soil cores of 2.5 cm diameter were collected from the top 10 cm at the conventional agriculture sites with corn/soybean/wheat crop rotation (rotation), deciduous forests (forest), soybean monoculture cropland (soybean) and a control treatment that was regularly tilled to remove vegetation (barren). The conventional agriculture and deciduous forests are part of the LTER Main Cropping System Experiment while the soybean monoculture and barren sites are within the Biodiversity Gradient Experiment. Winter wheat was the crop at the conventional agriculture sites when the soil was sampled. The litter layer in the deciduous forest soil was removed prior to sampling. For each biome, soil cores were collected from three experimental sites in June, August and September. Soil cores were also collected from the rotation and forest sites in March, May, and December to determine if there is a seasonal variation in BGE. The soil cores from each experimental site were pooled in a Whirl-Pak bag and brought back to lab on ice. The soil was homogenized with a 4 mm sieve and stored at 12 °C until used for experiments. All measurements were made within 48 h of soil sampling. Soil pH and moisture were determined prior to start of experiments according to standard methods (Robertson et al., 1999). Soil subsamples were also frozen at −80 °C for chemical analysis.

### 2.2. Soil chemistry

Water-soluble dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were extracted using a protocol modified from Jones and Willett (Jones and Willett, 2006). Briefly, 2 g frozen soil samples were suspended in 20 ml sterile deionized water supplemented with sodium pyrophosphate. The soil slurry was shaken at 200 rpm for 30 min followed by centrifugation at 8000 *g* for 10 min. All steps were performed at 4 °C to reduce decomposition. The supernatant fraction was filtered through a 0.45 μm syringe filter to remove particulate organic matter, including most bacteria. DOC and TDN were measured using a Shimadzu TOC-TN analyzer (Shimadzu, Columbia, MD), courtesy of Dr. Steve Hamilton at KBS.

### 2.3. Soil slurries

The preparation of soil slurries for bacterial production (BP) and bacterial respiration (BR) measurements is depicted in Supplementary Fig. S1. Soil slurries were prepared by suspension of 10 g field moist soil sample in 10 ml 10 mM MES buffer. The buffer pH was prepared according to the soil pH and was supplemented with 50 μg/ml cycloheximide to inhibit fungal growth and 2.3 mM sodium pyrophosphate to assist with dispersion of microbes. While archaea are not necessarily inhibited by cycloheximide, they are present in very low abundance in KBS LTER soils, contributing only 1.4% of the total rRNA sequences (Buckley et al., 1998). The soil suspension was homogenized for 30 mins at 200 rpm and then filtered through 8