

Microbial residues as indicator for inorganic carbon transition to organic carbon in coastal saline soils

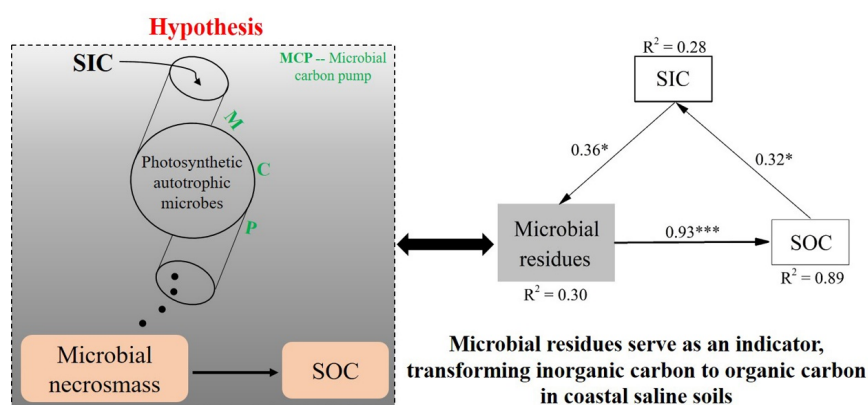
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Abstract

Although autotrophic or chemotrophic microorganisms can assimilate CO₂ or carbonate, it is still unclear how microorganisms convert soil inorganic carbon (SIC) to organic carbon (SOC), owing to the lack of a microbial indicator between SIC and SOC. Herein, we hypothesized that carbonate-rich saline soils are a potential source that contribute to the SOC pool through the transformation of microbial necromass. SIC levels linearly decreased with an increase in salinity, while SOC and microbial residues exponentially declined. A structural equation model verified the causality of SIC-microbial residues-SOC, suggesting that microbial residues can serve as an indicator of SIC transition to SOC. This study highlights the regulation of microbial necromass in SIC cycling, thus enhancing the application of SIC for C biogeochemical cycles and enriching organic C reservoirs in global saline or dry lands.



Introduction

Soil inorganic carbon (SIC), usually as a “missing C sink”, accounts for 60–80% soil C stocks, and essentially influences soil C cycles in saline or dry lands (Mi et al., 2008; An et al., 2019). SIC can be converted to soil organic carbon (SOC), providing organic C source to soil organisms (Groshans et al., 2018). Although plant assimilated inorganic C is the major SOC source that atmospheric and soil-released CO₂ fixed via photosynthesis contributes to the SOC pool through litter and root input (Figure 1, Le Quéré et al., 2018), microorganisms potentially contribute to the conversion of SIC to SOC (Miltner et al., 2004; Liu et al., 2020b). Thus, it is important to speculate the potential mechanisms in the microbially driven SIC-to-SOC transition, thus facilitating soil C efflux and improving soil fertility in resource-limited saline lands.

Most microbes use organic matter as energy for reproduction and growth, contributing to the SOC pool through microbial cell residues (Kögel-Knabner, 2017; Ni et al., 2020). However, certain microbes, e.g., photosynthetic bacteria, potentially use SIC (mainly carbonate) as C source to synthesize cell (Zamanian et al., 2016; Moore et al., 2020). $^{13}\text{CO}_2$ incubation experiments have reported that soil autotrophic microorganisms can utilize inorganic C to synthesize microbial biomass (Perez and Matin, 1982; Miltner et al., 2004). Although living microbial biomass constitute only 2–4% of SOC (Dalal, 1998), rapid, iterative microbial cell growth and death generate sizable microbial necromass entombing in soils, accounting for > 50% SOM (Kallenbach et al., 2016; Liang et al., 2019). Furthermore, Liang et al. (2017) proposed the concept of a microbial carbon pump (MCP), providing novel mechanistic insights into SOM formation involved in microbial anabolism. Such knowledge and the MCP concept would help predict microorganisms converting SIC to SOC via microbial necromass (Fig. 1).

A systematic field survey was performed to explore the shift in soil C components (i.e., SIC, SOC, and microbial residues) along a natural salinity gradient. Microbial residue mediation in soil C transformation was evaluated using biomarkers including amino sugars. We aimed to examine whether the trends in soil C components were consistent from low to high salinity determine the mechanism underlying SIC—microbial residues—SOC.

Materials and methods

In August 2017, we evaluated 94 sites of saline land in Yellow River Delta (37°33'–38°09'N, 118°35'–119°13'E), China, with 0.50–19.24 salinity (Fig. S1), and pH 7.04–8.08 (Fig. S2). Vegetation types primarily included crops (maize, cotton etc.), *Phragmites*, *Tamarix chinensis*, *Suaeda salsa*, and mudflat.

Five soil cores were randomly collected at each site, pooled, and homogenized into a representative soil sample. Soil $\text{pH}_{(1:2.5 \text{ w/v})}$ was determined using a pH meter; total soluble salinity concentration measured by gravimetric method with water extraction (Chi et al., 2019). Carbonate was determined by Acid-base titration, representing SIC (Fu et al., 2020); SOC was analyzed on a Vario MACRO Cube (Elementar, Langensfeld, Germany) after removing SIC with hydrochloric acid. Amino sugars and microbial residues were analyzed using previously reported methods (Zhang and Amelung, 1996; Engelking et al., 2007).

Generalized linear regression models were developed to assess associations among SIC, SOC, and microbial residues (R software). Structural equation modeling (SEM) was performed to trace causality among SIC, microbial residues, and SOC via root-mean-square error of approximation (AMOS software).

Results and discussion

Along the natural salinity gradient, the SIC was higher at low salinity, < 6 suggesting that salinity stress influences SIC cycling (Wang et al., 2019). SIC has two potential determinants: (1) uptake and deposition of atmospheric CO_2 by base cation (Xie et al., 2009; Raheb et al., 2017), and (2) re-distribution of respired CO_2 among microorganisms and roots (Huber et al., 2019). pH markedly influences the magnitude of SIC, soil acidity at low pH results in SIC loss, and soil alkalinity at high pH increases atmospheric and soil CO_2 absorption of base cations (Liu et al., 2020a; Raza et al., 2020). Slight pH alterations under different saline conditions indicate that SIC alterations are not attributed to regional atmospheric CO_2 deposition (Fig. S2). Furthermore, SOM accumulation due to improved plant communities may increase microbial and root respired CO_2 , retaining SIC via base cation absorption (Lal and Kimble, 2000). Highly photosynthetic crops and *Phragmites* in low-salinity soil results in higher SIC and SOC than with low-photosynthetic *Tamarix chinensis* and *Suaeda salsa* in high-salinity soil (Xia et al., 2019; Fig. S3, Fig. S4). Thus, SIC is increased through changes in organic matter decomposition, further verified through the direct effect of SOC on SIC (Fig. 2c).

Low-salinity soil contains more SOC, displaying a substantial decline at high salinity of > 6 pointed that plant- and microbially-induced C drive SOC storage via litter decomposition and OM transformation (Schmidt et al., 2011; Ding et al., 2019). Plants displaying high-to-low photosynthetic C fixation and the consistent trend between microbial residues and SOC indicate that plant and microbial residues increase SOC storage

with increasing salinity (Fig. 2a). However, it is still unclear whether other soil C components linking inorganic or organic biogeochemical processes as potential determinants of SOC accumulation, e.g., SIC (primarily carbonate) account for soil C in approximately 70% of these regions. We assume that SIC not only provides C source to autotrophic microorganisms (e.g., cyanobacteria) (Moore et al., 2020), but also serves as a “reserving SOM source” via bio-transformation (Miltner et al., 2004). Significantly linear associations among microbial residues, SOC, and SIC indicate that SIC is a potential determinant of SOC components (Fig. 2b). Furthermore, SEM helped determine the causality and underlying mechanism of SIC-microbial residues-SOC (Fig. 2c), suggesting microbial residues as an indicator for SIC transition to SOC, and verifying our hypothesis.

Despite regulation of terrestrial C cycles through two microbial metabolic processes, i.e., atmospheric and soil C release through microbial catabolism and respiratory CO₂ fixation into carbonate via base cation absorption (Zhao et al., 2020), microbial anabolism-derived C contributes to the SOC pool (Liang et al., 2017). To better understand soil C cycling, this study describes microbial SIC-SOC conversion, which is important to understand the role of SIC in C cycling in terrestrial ecosystems. SIC generally serves as a potential C sink and limited information is available regarding its effect on terrestrial C-energy process because of its long-term persistence, high stability, and limited bio-availability (few biomes use SIC as resources) (Zamanian et al., 2018; Liu et al., 2020b). We report the contribution of SIC to SOC stocks, indicating that SIC provides inorganic C-source for other soil biomes after conversion from autotrophic microorganisms. We could not determine the relevant microbial communities or determine the magnitude of the SIC-to-SOC transition. Future studies need to investigate the association between genomic and metabolomic factors *in vitro* and *in situ*, especially on the molecular and metabolic process involved in the microbial SIC metabolism and assimilation and the mechanisms followed by specific microbial species, using ¹³C-labeled CO₂ or carbonate. Moreover, understanding the role of microbial necromass in SIC transition would enhance SIC applications for C biogeochemical cycles in global saline and dry lands, accounting for the provision of “missing C” to enrich the organic C reservoir through interactions among SIC-microbial metabolites-SOC.

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Figure legends

Fig. 1 Conceptual diagram describing biologically driven soil organic (SOC) and inorganic carbon (SIC) cycling. SOC sources from plant litter and root exudates and SIC sources from respired CO₂ among microorganisms and roots are highlighted (left diagram); and we hypothesize that microbial necromass play a role in SIC-to-SOC transition in accordance with the microbial carbon pump theory (right diagram).

Fig. 2 C components (i.e., soil inorganic carbon [SIC], soil organic carbon [SOC], and microbial residues) of coastal saline soils (n=94) in Yellow River Delta. (a) The shifts in SIC, SOC, and microbial residue levels along a natural salinity gradient; (b) associations among SOC, microbial residues, and SIC; (c) structural equation modeling examining the underlying causal relationships among SIC, microbial residues, and SOC.

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