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Straw-returning reduces the contribution of microbial anabolism to salt-affected soil organic carbon accumulation over a salinity gradient

Yingdong Huo, Guoqing Hu*, Xu Han, Hui Wang, Yuping Zhuge

National Engineering Research Center for Efficient Utilization of Soil and Fertilizer Resources, College of Resources and Environment, Shandong Agricultural University, Taian 271018, China

* Corresponding author. E-mail: huguotsing@163.com (G. Hu)

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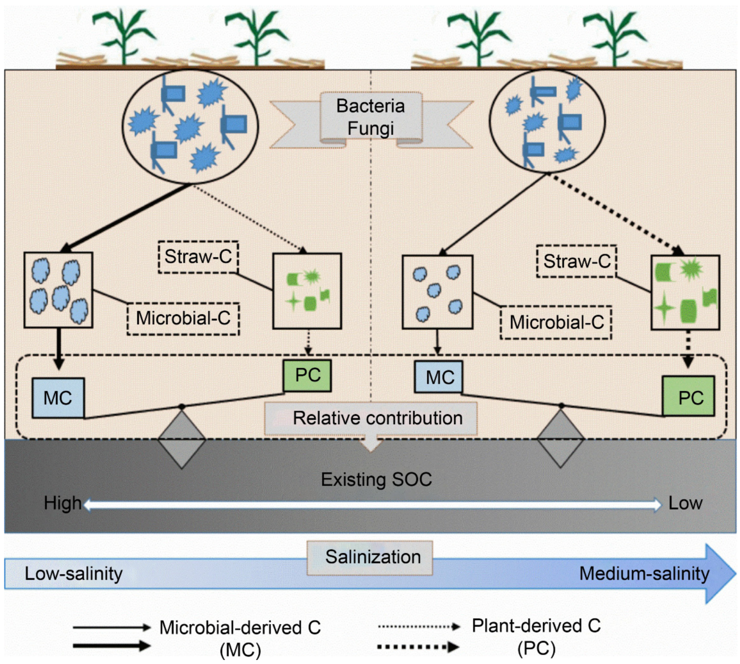
ABSTRACT

- In low-salinity soil, straw-returning did not change necromass contribution to SOC.
- In medium-salinity soil, straw-returning reduced necromass contribution to SOC.
- Straw-returning reduced POC contribution to SOC in low-salinity soil.
- Straw-returning increased POC contribution to SOC in medium-salinity soil.
- Salinity affects the contribution of microbial-derived and plant-derived C to SOC.

Salinization affects microbial-mediated soil organic carbon (SOC) dynamics. However, the mechanisms of SOC accumulation under agricultural management practices in salt-affected soils remain unclear. We investigated the relative contribution of microbial-derived and plant-derived C to SOC accumulation in coastal salt-affected soils under straw-returning, by determining microbial necromass biomarkers (amino sugars) and particulate organic C (POC). Results showed that, straw-returning increased necromass accumulation in low-salinity soil but did not change its contribution to SOC. In medium-salinity soil, straw-returning did not increase necromass accumulation but decreased its contribution to SOC. In low- and medium-salinity soils, the contribution of POC to SOC showed the opposite direction to that of the necromass. These results suggest that under straw-returning, the relative contribution of microbial-derived C to SOC decreased with increasing salinity, whereas the reverse was true for plant-derived C. Our results highlighted that straw-returning reduces the contribution of microbial anabolism to SOC accumulation in salt-affected soils with increasing salinity.



Keywords amino sugars, crop straw-returning, soil organic carbon, particulate organic carbon, soil salinization

1 Introduction

Soil salinization is one of the major global environmental and socioeconomic concerns (Hassani et al., 2021). It decreases plant biomass, consequently reducing the plant inputs of soil organic carbon (SOC) (Setia et al., 2013). Soil microorganisms are crucial to the conversion of plant matter to SOC through metabolic processes (Schimel and Schaeffer, 2012). It has been reported that salinization markedly affects microbial activities, biomass, and communities (Rath et al., 2019). However, the mechanisms of SOC accumulation under agricultural management practices, such as straw-returning, in salt-affected soils are not comprehensively understood.

During plant matter decomposition, some partially

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decomposed plant debris is typically considered to be predominant regarding the formation of particulate organic C (POC) and directly contributes to SOC accumulation (Witzgall et al., 2021; Cotrufo et al., 2022). However, increasing evidence suggests that microbial anabolism may contribute more to SOC storage in the form of microbial necromass (Liang et al., 2017; Klink et al., 2022). Recently, accumulation of fungal and bacterial necromasses in salt-affected soils was found to depend on salinity (Chen et al., 2021; Shao et al., 2022). POC content, which is mostly of plant origin (Jilling et al., 2020), is significantly affected by salinity under straw-returning (He et al., 2022). Therefore, simultaneously assessing the contributions of microbial necromass and POC to the SOC pool under straw-returning can help determine the relative contribution of microbial and plant-derived C to SOC accumulation (Zhu et al., 2020; Cotrufo et al., 2022).

Soil amino sugars are reliable biomarkers of microbial necromass because they are absent in plants, thus they can be used to assess the contribution of microbial necromass to SOC storage at the community level (Joergensen, 2018; Zhu et al., 2020). In this study we determined amino sugars and POC in four coastal saline soils with two salinity levels (low and medium) and two straw-returning treatments. The objective of this study was to assess the influence of straw-returning on the accumulation of microbial necromass and POC in salt-affected soils and then to evaluate the relative contribution of microbial- and plant-derived C to SOC accumulation. We hypothesized that (1) straw-returning should increase the accumulation of microbial necromass, regardless of the salinity level, whereas (2) decrease the contribution of microbial-derived C (by microbial anabolism) to SOC accumulation with increasing salinity.

2 Materials and methods

2.1 Study site and sampling

We collected soil samples at the Wudi Experimental Station of Shandong Agricultural University (37°55–56' N, 117°55–57' E), which is located in the Yellow River Delta, Shandong Province, China. This region has a mean annual temperature of 11.5°C and a mean annual precipitation of 600 mm. The soils were classified as Fluvic Cambisols (Word Reference Base). Since winter wheat and summer maize could not be planted under high salinity (> 4 dS m^{-1}) conditions, this experiment used soils with low salinity ($EC_{5:1}$ 1.3 dS m^{-1}) and medium salinity ($EC_{5:1}$ 2.3 dS m^{-1}) in October 2014 (He et al., 2022). Straw-returning and no straw-returning treatments with three replicates were conducted on each soil, following a winter wheat-summer maize rotation system (Table 1). The straw-returning methods, straw-returning amounts, and chemical fertilizer application rates are shown in Table 1. On 30 September 2017, soil samples were collected from each soil type using a 5-cm-diameter soil auger to a depth of 20 cm.

2.2 Soil chemical analysis

Soil pH was measured in a 2.5:1 water–soil suspension using a pH meter. Soil electrical conductivity (EC) was determined in a 5:1 water–soil suspension using a conductometer. The content of SOC was determined using the $K_2Cr_2O_7$ oxidation method (Bao, 2005). The content of soil total nitrogen (TN) was determined using a CN analyzer (Vario Macro Elementar, Germany).

2.3 Soil amino sugar and particulate organic carbon analysis

Microbial necromass was determined using amino sugar analysis (Zhang and Amelung, 1996). Concentrations of three amino sugars, including glucosamine (GluN), galactosamine (GalN), and muramic acid (MurN), were determined. Total amino sugars (TAS) were calculated as the sum of GluN, GalN, and MurN. Particulate organic matter was separated according to Cambardella and Elliott (1992). POC content was determined using the $K_2Cr_2O_7$ oxidation method (Bao, 2005).

2.4 Statistical analysis

Two-way analysis of variance was used to test the effects of salinity, straw-returning, and their interaction effects on soil

Table 1 The crop rotation system, straw returning amount and fertilizer application rate in this experiment.

Saline soil type	Farming management	Crop rotation system	Straw-returning amount per year (wheat + maize) (t hm^{-2})	Fertilizer application rate per growing season (N-P_2O_5-K_2O) (kg hm^{-2})
Low-salinity soil	No straw-returning	Winter wheat-summer maize	–	225-150-75
	Straw-returning*	Winter wheat-summer maize	12.7	225-150-75
Medium-salinity soil	No straw-returning	Winter wheat-summer maize	–	225-75-75
	Straw-returning*	Winter wheat-summer maize	7.3	225-75-75

Note: * straw-returning methods were consistent with local habits, that is, returning wheat straw mulch and maize straw plow (with a plowing depth of 15 cm).

physiochemical properties, amino sugars, and POC, as well as their contribution to SOC by SPSS25.0. An independent-sample *t*-test was used to compare the differences in the contribution of necromass C or POC to SOC between low- and medium-salinity soils and between those with and without straw-returning treatments by SPSS25.0 ($p < 0.05$, $p < 0.01$).

3 Results and discussion

GluN, GlaN, and TAS content decreased ($p < 0.05$), whereas MurN content increased at higher salinity ($p < 0.05$; Table 2). Under straw-returning, low-salinity soil showed improved GluN and TAS content (Table 2); however, medium-salinity soil indicated no differences in individual amino sugar and TAS contents. The GluN/MurN ratio decreased from low to medium-salinity soils but showed no significant difference under straw-returning. GluN-C/SOC decreased as salinity increased, whereas MurN-C/SOC increased ($p < 0.05$; Fig. 1). Straw-returning did not change GluN-C/SOC, MurN-C/SOC, and TAS-C/SOC in low-salinity soils ($p > 0.05$), but decreased GluN-C/SOC, GlaN-C/SOC, MurN-C/SOC, and TAS-C/SOC in medium-salinity soils ($p < 0.05$).

Our results suggested that total microbial necromass accumulation decreased significantly with increasing salinity, whereas contrasting trends were observed for fungal and bacterial necromasses. This was consistent with the results of Chen et al. (2021), demonstrating that salinity is a key factor affecting microbial necromass accumulation (Yan et al., 2021). Interestingly, straw-returning increased the total microbial necromass accumulation in low-salinity soil, primarily due to the increase in fungal necromass; however, there was no significant difference in fungal and bacterial necromasses in medium-salinity soil (Table 2). These findings indicate that straw-returning can improve microbial anabolism in low-salinity soil, especially with respect to fungal anabolism (Muhammad et al., 2006; Liu et al., 2019). By contrast, higher salinity limits microbial anabolism, which may be due to suppressed microbial activities and lower microbial straw-C use efficiency, under salt stress (Chowdhury et al., 2011; Rath and Rousk, 2015; Zhang et al., 2019).

Straw-returning did not change the contribution of microbial necromass to SOC in low-salinity soil, whereas in medium-salinity soil, it reduced this contribution (Fig. 1). In low-salinity soil, microbial necromass accumulated at the same rate as SOC indicated that microbial anabolism had a synergistic effect with SOC accumulation (Liang et al., 2019; Klink et al., 2022). However, the decrease in the ratio of amino sugars to SOC suggested that the relative contribution of microbial anabolism to SOC accumulation decreased in medium-salinity soil. We found that straw-returning had no effect on POC content but reduced its contribution to SOC in low-salinity soil (Fig. 2). However, in medium-salinity soil, straw-returning increased POC content, and its contribution to SOC. POC is assumed to be dominated by partially decomposed plant residues (Paul et al., 2013; Cotrufo et al., 2019). Thus, our results suggest that plant-derived C may play a more important role in SOC accumulation in medium-salinity soil than in low-salinity soil (Wichern et al., 2006; He et al., 2022).

Our results, based on the combination of source-specific amino sugars and POC analyses, reflect the relative contribution of microbial and plant-derived C to SOC accumulation

Table 2 Selected soil properties in coastal salt-affected soils with low- and medium-salinity under straw-returning.

Saline soil type	Farming management	$pH_{water:soil=2.5:1}$	$EC_{water:soil=5:1}$ (dS m^{-1})	SOC (g kg^{-1})	TN (g kg^{-1})	GluN (mg kg^{-1})	GalN (mg kg^{-1})	MurN (mg kg^{-1})	TAS (mg kg^{-1})	GluN/ MurN
Low-salinity soil	No straw-returning	8.11	1.28	10.02	0.83	301.80	144.77	82.90	529.47	3.63
	Straw-returning	8.17	1.23	12.05	0.98	333.80	155.80	91.57	581.17	3.67
Medium-salinity soil	No straw-returning	8.32	2.31	8.65	0.90	217.33	116.10	104.90	438.40	2.07
	Straw-returning	8.29	2.29	11.70	0.87	242.13	120.73	111.13	474.03	2.17

ANOVA (*p*-values)	$pH_{water:soil=2.5:1}$	$EC_{water:soil=5:1}$ (dS m^{-1})	SOC (g kg^{-1})	TN (g kg^{-1})	GluN (mg kg^{-1})	GalN (mg kg^{-1})	MurN (mg kg^{-1})	TAS (mg kg^{-1})	GluN/ MurN
Saline soil type (S)	**0.022**	**0.000**	**0.024**	0.124	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Farming management (F)	0.846	0.612	**0.000**	0.583	**0.017**	0.076	0.078	**0.007**	0.751
S×F	0.495	0.851	0.140	**0.042**	0.715	0.429	0.750	0.523	0.873

Note: EC, electrical conductivity. SOC, soil organic carbon. TN, soil total nitrogen. GluN, glucosamine (is representative of fungal necromass). GalN, galactosamine (is generally considered to be derived from bacteria). MurN, muramic acid (represents bacterial necromass). TAS, Total amino sugars were, calculated as the sum of GluN, GalN, and MurN (represents total microbial necromass). GluN/MurN, is generally used to evaluate the relative accumulation of fungal and bacterial necromass. The sign "×" indicates a term interaction.

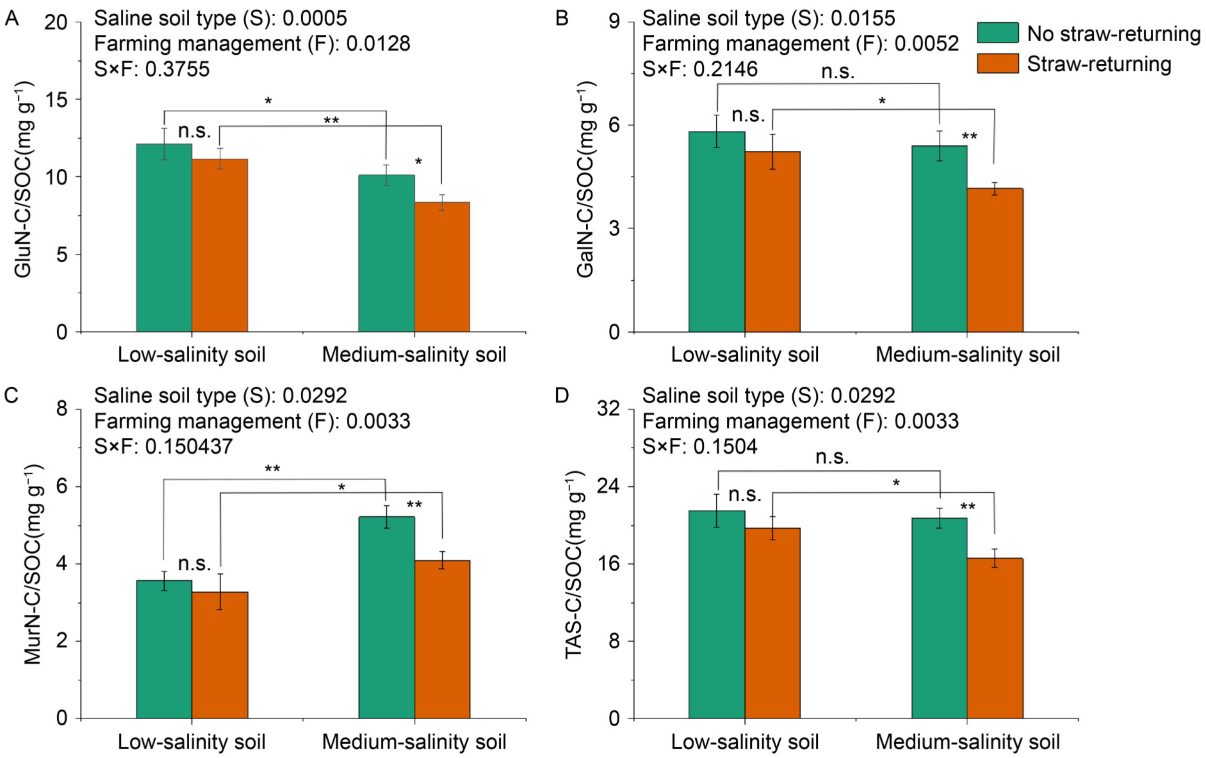

Fig. 1 Contributions of glucosamine C (GluN-C), galactosamine C (GalN-C), muramic acid C (MurN-C), and total amino sugar C (TAS-C) to soil organic carbon (SOC) in the soils with different salinity levels. (A) Contribution of GluN-C to SOC, (B) Contribution of GalN-C to SOC, (C) Contribution of MurN-C to SOC, (D) Contribution of TAS-C to SOC. Error bars are standard deviation (n = 3). Different letters represent significant differences between the no straw returning and straw returning treated soils within each soil treatment (t-test; *$p < 0.05$, **$p < 0.01$).

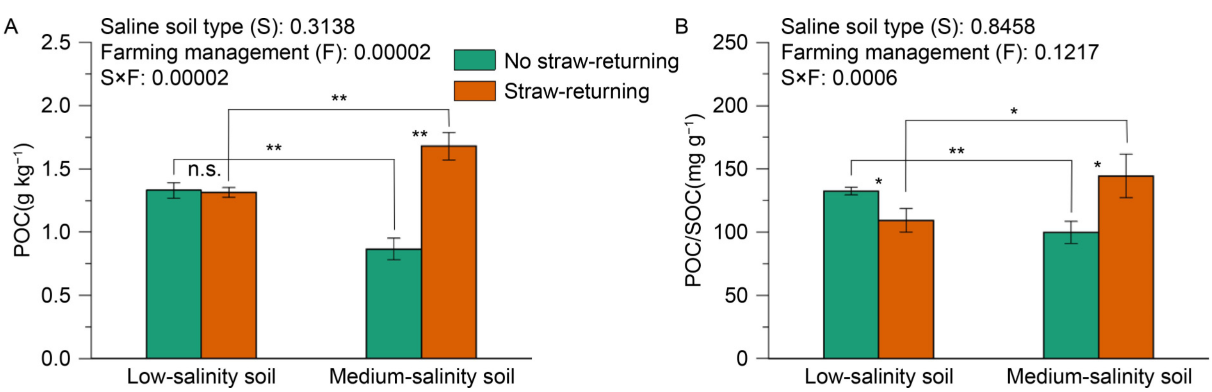

Fig. 2 POC contents (A) and their contributions to SOC (B) in the soils with different salinity levels. POC, particulate organic carbon; SOC, soil organic carbon. Error bars are standard deviation (n = 3). Different letters represent significant differences between the no straw-returning and straw-returning treated soils within each soil treatment (t-test; *$p < 0.05$, **$p < 0.01$).

in low and medium-salinity soils. The results are described using a framework (Fig. 3). As salinity increased, the relative contribution of microbes to SOC accumulation decreased, whereas that of plants increased significantly. Therefore, the SOC-increasing mechanisms in low and medium-salinity soils were remarkably different under straw-returning. Considering the differences in the stability of microbial necromass and POC (Dippold et al., 2018; Cotrufo and Lavallee, 2022), future research should focus on SOC stability during crop residue management of salt-affected soils over gradients of salinity.

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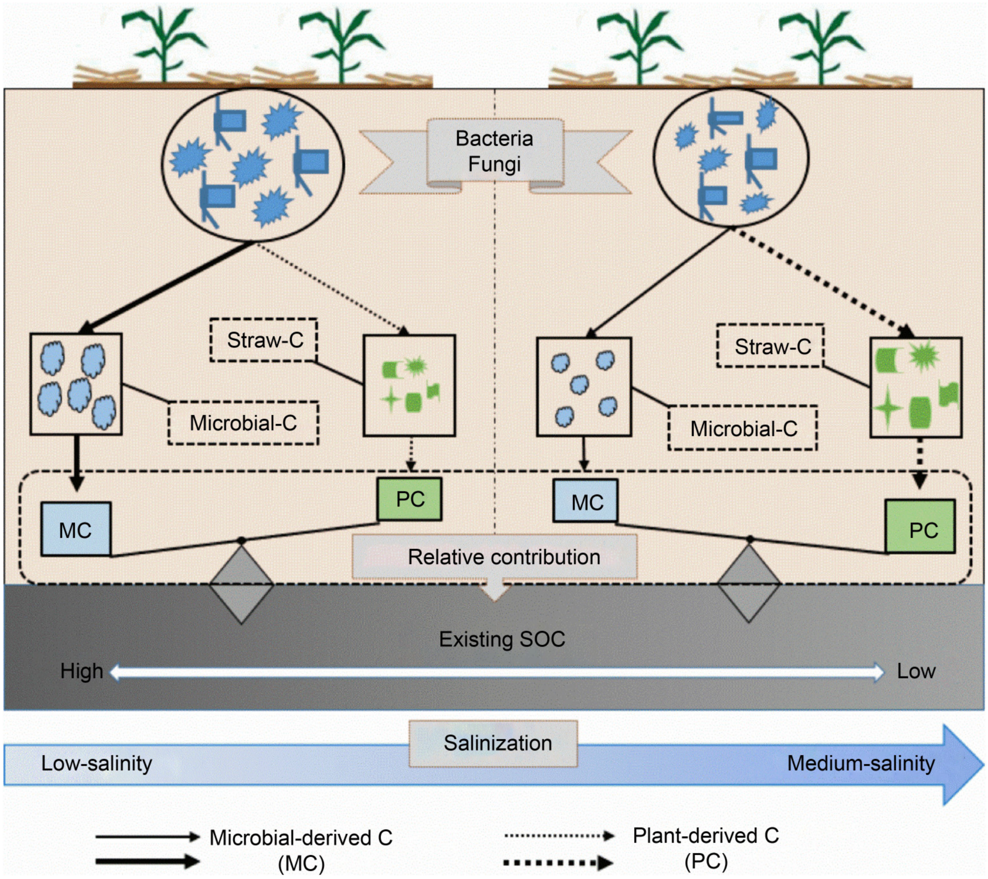

Fig. 3 A simplified illustration of the framework demonstrating the relative contribution of microbes and plants to SOC accumulation under straw-returning over a salinity gradient.

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