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RESEARCH ARTICLE

Granulated straw incorporation efficiently promotes soil organic carbon pool in subtropical infertile croplands primarily *via* plant residues accumulation

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Highlights

- Massive granulated straw incorporation into infertile croplands effectively enhances soil organic carbon (SOC) pool and crop yield.
- As granulated straw incorporation increases, SOC accumulation efficiency varies from 30.8 to 60.0%.
- SOC increases under granulated straw incorporation primarily originate from plant residues rather than microbial necromass.

Abstract

Rapidly improving infertile croplands and enhancing their soil organic carbon (SOC) pool necessitate substantial organic materials incorporation. Converting loose crop straw into granulated form facilitates uniform incorporation within the plough soil layer. As an innovative soil amelioration approach, the efficiency and patterns of SOC accumulation remain unclear. Two field experiments were conducted in infertile subtropical upland and paddy soils with 0, 30, 60, and 90 Mg ha^{-1} granulated straw incorporation. After one year, SOC accumulation efficiency from straw input remained stable in upland (30.8–37.5%) with increasing amounts of straw incorporation, while declined from 60.0 to 38.3% in paddy. In both croplands, the contributions of lignin phenols to SOC increased with increasing straw incorporation, while the contributions from amino sugars remained constant at higher straw input levels. Subsequently, the ratios of lignin phenols to amino sugars increased with increasing straw incorporation, indicating faster plant residue accumulation compared to microbial necromass, as the granulation approach limited microbial involvement in straw transformation. Thus, single-time incorporation of substantial granulated straw presents an effective agricultural strategy for rapid amelioration of infertile croplands.

Keywords: SOC accumulation efficiency, granulated straw, upland and paddy, plant residues, microbial necromass, microbial community

1. Introduction

Low- and medium-fertility croplands constitute 68.8% of China's total agricultural land (Zhang and Li 2023). Infertile croplands, characterized by low soil organic carbon (SOC) levels, are prevalent across major grain-producing regions (He *et al*. 2018). Rapid improvement of these infertile croplands presents significant potential for increasing crop yield (Xu *et al*. 2022; Wang *et al*. 2024). The incorporation

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of crop residues into croplands represents a common agricultural practice for enhancing SOC content and soil fertility (Tian *et al.* 2015; Berhane *et al.* 2020; Li *et al.* 2023). However, traditional *in-situ* incorporation of chopped crop straw increases SOC by only 11.5% over 1–2 years across major climate zones in China (Wang *et al.* 2021). This modest increase proves insufficient for rapid amelioration of infertile croplands, particularly in southern China, where high temperature and humidity accelerate organic matter decomposition. The low-density and loose nature of crop straw impedes uniform incorporation of large quantities into the plough layer. Converting chopped straw into rod-shaped granules substantially increases its density, enabling efficient incorporation into cropland soils (Cong *et al.* 2020; Fan and Wu 2020; Wang *et al.* 2024). Considering the extensive infertile croplands in Southern China, understanding SOC responses to granulated straw incorporation becomes essential.

Within conventional chopped straw incorporation rates (5–15 t ha^{-1}), SOC accumulation typically exhibits a linear relationship with incorporated straw quantity (Kong *et al.* 2005; Wang *et al.* 2018; Lin *et al.* 2022). However, as the SOC pool approaches saturation capacity, SOC accumulation efficiency decreases with increasing straw incorporation due to limited reactive mineral surfaces (Six *et al.* 2002; Stewart *et al.* 2009; Li *et al.* 2023). Additionally, increased straw input reduces microbial C use efficiency, limiting SOC accumulation efficiency (Wang *et al.* 2025), due to microbial nutrient limitations arising from straw's high C/nutrient ratio compared to soil conditions (Sinsabaugh *et al.* 2013; Chen *et al.* 2021). Unlike chopped straw, granulated straw undergoes substantial physical alterations, potentially restricting microbial access and modifying microbial C utilization (Fan *et al.* 2023). Nevertheless, the patterns of SOC and its components accumulation under varying granulated straw incorporation levels remain inadequately studied.

Incorporated straw is partially assimilated by soil microorganisms for biomass synthesis (Sinsabaugh *et al.* 2013; Chen *et al.* 2020), and transforms into microbial necromass through cell growth-death processes, ultimately accumulating in soils (Liang *et al.* 2019). The remaining straw undergoes extracellular enzymatic decomposition and physicochemical stabilization before preservation as plant residues in soil (Cotrufo *et al.* 2015). Microbial C transformation processes differ markedly between upland and paddy soils due to contrasting moisture conditions (Duan *et al.* 2024a, b). Straw-C accumulation is generally lower in upland compared to paddy soils due to enhanced microbial catabolism under well-drained conditions, resulting in greater microbial necromass contribution to SOC accumulation (Chen *et al.* 2021). Compared to traditional practices, the granulation approach may reduce microbial necromass contribution to SOC accumulation by limiting microbial accessibility to the straw (Fan *et al.* 2023). However, this hypothesis and its variations between paddy and upland soils require further investigation.

This study conducted two micro-plot field experiments in subtropical China to ameliorate infertile upland and paddy soils. The research examined SOC accumulation efficiency and the accumulation patterns of microbial necromass and plant residues through granulated straw incorporation. The study tested three hypotheses: (i) SOC accumulation efficiency decreases with increased granulated straw incorporation as soils approach C saturation; (ii) plant residue accumulation efficiency exceeds that of microbial necromass because straw granulation limits microbial attachment to straw particles and inhibits microbial metabolism through physical spatial isolation; (iii) SOC accumulation efficiency is lower in upland compared to paddy soil due to enhanced microbial metabolism under well-drained conditions.

2. Materials and methods

2.1. Site description

The experimental site was situated at the Changsha Research Station for Agricultural and Environmental Monitoring in Jinjing Town, Changsha County, Hunan Province, China. The region experiences a subtropical monsoon climate, with an annual mean temperature of 17.5°C and precipitation of 1,330 mm. The study utilized low-fertility upland and paddy for micro-plot experiments. The upland and paddy fields are situated at altitudes of 82.7 and 92.3 m, respectively, with a straight distance of 1.3 km between them. The upland soil, derived from granite parent material, comprises 7.1 g kg^{-1} organic C, 1.2 g kg^{-1} total N with a C/N ratio of 5.9, 0.2 g kg^{-1} total P, 20% clay, 38% silt, 42% sand, and pH of 7.2. The paddy soil, originating from shale parent material, contains 9.6 g kg^{-1} organic C, 1.0 g kg^{-1} total N with a C/N ratio of 9.6, 0.72 g kg^{-1} total P, 28% clay, 48% silt, 24% sand, and pH of 6.1. The C saturation degree reached 17.6 and 27.1% in upland and paddy soils, respectively. The calculation details appear following the methodology described by Six *et al.* (2002).

2.2. Materials preparation

Rice straw underwent compression to create granulated forms. The granulation process involved: i) crushing rice straw into 2–5 cm length fragments using a crusher; ii) adding appropriate nutrients to reduce microbial nutrient limitation (Duan *et al.* 2025); iii) adjusting mixture moisture content to 10–15%; iv) granulating the mixtures into particles of 6–8 mm diameter and 5–6 cm length using a granulator. The granulated straw achieved a final density of 0.50–0.55 g cm^{-3}, approximately 16 times greater than chopped straw.

The field setup utilized stainless frames measuring 0.8 m×0.8 m×0.3 m (length×width×height) to isolate each micro-plot. Adjacent stainless-steel frames maintained approximately 5 cm spacing to prevent contamination of soil dissolved organic carbon and nutrients. Each micro-plot contained two sections: (i) crop growth monitoring area, (ii) soil fertility and nutrient release monitoring area. Appendix A presents the detailed micro-plot design.

2.3. Experimental design

The micro-plot experiments for both upland and paddy commenced in April 2022. To determine optimal dosage for SOC and crop yield improvement, 0, 30, 60, and 90 Mg ha^{-1}

of granulated straw were incorporated in both experiments, targeting SOC content increases of 1.2, 2.4, and 3.6 g C kg^{-1} in the 0–25 cm layer, assuming a humification coefficient of 0.3 for new straw input (Tinsley and Darbyshire 1984). The experiment employed a randomized complete block design (RCBD) with four treatments, each replicated three times. The procedure involved thoroughly mixing 250 kg fresh soils (representing total soils from 0–25 cm depth) from each micro-plot with the designated amount of granulated straw in a large plastic container, then returning the mixtures to corresponding micro-plots. Maize and dry-rice were cultivated in the crop growth monitoring areas of upland and paddy micro-plots, respectively. Dry-rice received moist irrigation during growth based on preliminary experimental findings (Appendix A).

Soil samples were collected from surficial layers (0–20 cm) at 30, 90, 180, and 360 days from the soil fertility and nutrient release monitoring areas. Each soil sample was divided into three portions. The first portion was immediately used for microbial biomass C measurement. The second portion was stored at −80°C for the analysis of phospholipid fatty acids (PLFAs) and microbial communities (bacteria and fungi). The remaining soil samples were air-dried for subsequent analysis. The air-dried samples collected on day 360 were analyzed for SOC, biomarkers of plant residues (lignin phenols), and microbial necromass (amino sugars). The grain yield and shoot biomass were determined at crop maturity.

2.4. Basic soil properties analysis

Soil pH was measured in 1:2.5 (w/v) of soil and deionized water using a laboratory pH meter (Mettler-pH 320, Mettler Toledo, Germany). Soil texture was determined using a laser particle size analyzer (Malvern Panalytical, Malvern, UK). SOC and total nitrogen (TN) were determined using a C and N elemental analyzer (Vario MAX cube-CNS, Germany). Total phosphorus was analyzed using the sodium hydroxide fusion method (Dick and Tabatabai 1977). Soil microbial biomass carbon (MBC) was determined using the chloroform fumigation-K_2SO_4 extraction method (Wu *et al.* 1990).

2.5. Lignin phenols and amino sugars analysis

Lignin phenols were quantified through alkaline CuO oxidation to release lignin monomers, followed by gas chromatography (Hedges and Ertel 1982). Specifically, 0.1 g soil was mixed with 0.5 g CuO, 100 mg ammonium Fe(II) sulfate hexahydrate [Fe $(NH_4)_2(SO_4)_2 \cdot 6H_2O$] and 0.4 mL internal standard (10 mg ethyl vanillin dissolved in 100 mL 2 mol L^{-1} NaOH solution) and 15 mL of 2 mol L^{-1} NaOH solution in Teflon vessel to break down lignin macro-molecules into monomer phenols. Lignin oxidation products were derivatized with N, O-bis-(trimethylsilyl) trifluoroacetamide (BSTFA) to yield trimethylsilyl (TMS) derivatives before quantification. Lignin phenols were quantitatively analyzed using an Agilent 6890A gas chromatograph (produced by Agilent Technologies, United States) equipped with a DM-1 column (30 m×0.25 mm×0.25 μm).

Microbial necromass was quantified by analyzing amino sugars following the method of Zhang and Amelung (1996). Amino sugars were extracted, purified, and converted to aldononitrile acetates. The derivatives were separated using an Agilent 6890A gas chromatograph equipped with an HP-5 capillary column and flame ionization detector. Individual amino sugars, including glucosamine (GlcN), galactosamine (Gala), and muramic acid (MurN), were detected by comparison with authentic standards and quality control according to the internal standard (myo-inositol). Total amino sugar content equals the sum of GlcN, Gala, and MurN.

Fungal necromass derived from glucosamine (F-GlcN) was calculated according to a molar GlcN to MurN ratio of 2:1 in bacteria (Engelking *et al.* 2007; Chen *et al.* 2018b). The calculations are as follows:

$$\text{F-GlcN (mg kg}^{-1}\text{)}=(\text{GlcN}/179.17-2\times\text{MurN}/251.23)\times 179.17$$

where F-GluN represents fungal-derived glucosamine; 179.17 and 251.23 represent the molecular weights (g mol^{-1}) of GlcN and MurN, respectively.

2.6. Microbial PLFAs analysis

The living microbial community was evaluated through phospholipid fatty acid analysis (Bossio and Scow 1998). In brief, soils underwent hydrolysis by adding a solution of chloroform:methanol:citrate buffer (1:2:0.8, v:v:v; pH=4.0) twice. Phospholipids were isolated from nonpolar lipids and converted into fatty acid methyl esters (FAMEs). The FAMEs were quantified using an Agilent 6890A gas chromatograph (Agilent Technologies, United States). The biomarkers for fungi include 16:1ω5c, 18:2ω6c and 18:1ω9c among fatty acids; the biomarkers for $Gram^+$ bacteria include i14:0, i15:0, i16:0, i17:0, i18:0, i15:1ω6c, i17:1ω9c, a15:0, a17:0; the biomarkers for G^- bacteria include 15:1ω6c, 16:1ω9c, 16:1ω7c, 17:1ω8c, 18:1ω7c, 18:1ω5c, cy17:0, cy19:0; the biomarkers for actinomycetes include 10Me16:0, 10Me17:0, 10Me18:0, 10Me17:1ω7c, 10Me18:1ω7c. Bacterial PLFAs represent the sum of $Gram^+$, $Gram^-$, and actinomycete PLFAs (Moorhead and Sinsabaugh 2006).

2.7. DNA extraction, Illumina sequencing, and sequence processing

DNA was extracted from 0.5 g of soil utilizing the TGuide S96 Magnetic Universal DNA Kit (Tiangen, China, DP812) to obtain nucleic acids (Appendix B). The DNA samples were amplified on the hypervariable V3–V4 region of the 16S rRNA gene using primers 338F (5′-ACTCCTACGGGAGGCAGCA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) for bacterial analysis (Klindworth *et al.* 2013). For fungal analysis, the ITS1 regions were amplified using ITS1F (5′-CTTGGTCATTTAGGAAGTAA-3′) and ITS2 (5′-GCTGCGTTCTTCATCGATGC-3′) primers (Gardes and Bruns 1993). Details of the PCR setup, cycling conditions, and sequencing processes are presented in Appendix B. The DNA sequences were deposited in the NCBI under accession number (PRJNA1206924).

2.8. Calculations and statistical analysis

SOC increase (g kg^{-1}) and SOC accumulation efficiency (%)

from straw input were calculated according to the following equations:

SOC increase=SOC_T–SOC_{CK}

SOC accumulation efficiency=(SOC_T–SOC_{CK})/Straw-C_{input}×100%

where SOC_T and SOC_{CK} represent the SOC contents (g kg^{-1}) of the treatments with granulated straw incorporation and the control after one year, respectively, and Straw-C_{input} denotes the C content of the incorporated granulated straw.

All analyses were conducted using R software (version 4.2.3) (https://cran.r-project.org/). Analysis of variance (ANOVA) for RCBD was performed using the "aov" function to evaluate the effects of granulated straw incorporation amount (0, 30, 60, and 90 Mg ha^{-1}) and block effects on SOC, lignin phenols, amino sugars, microbial PLFAs, and microbial diversity in upland or paddy soils. When significant treatment effects were detected (P<0.05), Tukey's post hoc test was implemented for multiple comparisons. The differences in these variables between paddy and upland soils under the same treatment were examined using an independent-sample t-test. The relationships between lignin phenols and amino sugars in SOC relative to microbial PLFAs and diversity were assessed through linear regression analysis using the "ggpmisc" packages. The associations between SOC biomarkers and microbial communities at the class level were analyzed using correlation analyses *via* the "corrplot" package.

3. Results

3.1. Crop yield and SOC accumulation

Following the incorporation of 30, 60, and 90 Mg ha^{-1} granulated straw, grain yield increased by 25.0, 55.6 and 83.3% in upland, and 46.4, 55.4 and 64.3% in paddy compared to their corresponding control, respectively (Table 1). Additionally, shoot biomass increased proportionally with straw incorporation amounts in both croplands (Table 1).

After one year, SOC increased by 1.4, 3.0 and 3.7 g kg^{-1} (equivalent to 32.3, 69.5 and 86.9%) in upland soil, and by 2.4, 3.9 and 4.6 g kg^{-1} (equivalent to 44.4, 72.2 and 85.2%) in paddy soil with increasing straw incorporation compared to their respective controls (Fig. 1-A and B). The SOC accumulation efficiency from straw input in upland soil ranged from 30.8 to 37.4% with no significant difference among the three straw input levels (Fig. 1-C). In contrast, the corresponding SOC accumulation efficiency in paddy soil decreased from 60.0 to 38.3% with increasing straw incorporation (Fig. 1-D).

Table 1 The grain yield and shoot biomass with 0, 30, 60, 90 Mg ha^{-1} granulated straw incorporation in upland and paddy in 2023

Landuse type	Treatment[1)]	Incorporation amount (Mg ha^{-1})	Crop yield (Mg ha^{-1})	Shoot biomass (Mg ha^{-1})
Upland	CK	0	3.6±0.1 d	5.9±0.8 c
	GS_{30}	30	4.5±0.1 c	7.6±1.0 b
	GS_{60}	60	5.6±0.4 b	9.7±0.4 a
	GS_{90}	90	6.6±0.3 a	10.6±0.8 a
Paddy	CK	0	5.6±0.7 c	7.6±0.6 c
	GS_{30}	30	7.0±1.3 b	8.7±1.1 b
	GS_{60}	60	8.7±0.3 a	9.1±1.1 b
	GS_{90}	90	9.2±0.8 a	10.0±1.0 a

[1)] CK, GS_{30}, GS_{60}, and GS_{90} represent 0, 30, 60, 90 Mg ha^{-1} of granulated straw incorporation, respectively.

During 2022, the study area experienced an extreme drought event that significantly impaired crop growth across all treatments. Consequently, only data from 2023 are presented. Lowercase letters indicate significant differences at P<0.05 among treatments in upland or paddy soil, as determined by ANOVA for randomized complete block design and Tukey's post hoc test.

3.2. Lignin phenols and amino sugars accumulation

With three levels of straw incorporation, the total lignin phenols content increased by 47.5, 74.4 and 234.1 mg kg^{-1} (equivalent to 75.1, 177.7 and 370.4%) in upland and 81.9, 155.8 and 273.1 mg kg^{-1} (equivalent to 178.1, 338.9 and 594.0%) in paddy compared to their respective controls

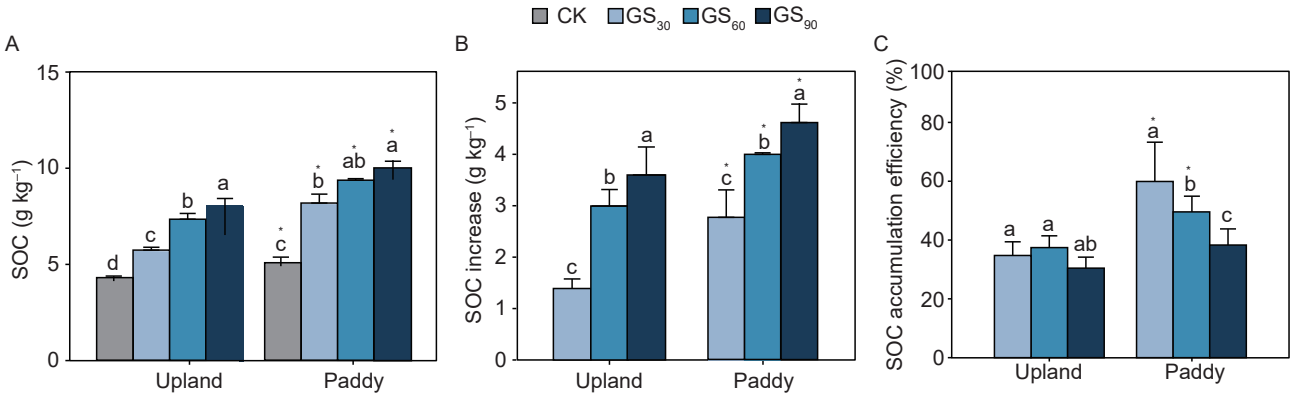


Fig. 1 Soil organic carbon (SOC) content (A), SOC increase (B), and SOC accumulation efficiency (C) following an one-year period of granulated straw incorporation in infertile upland and paddy soils. CK, GS_{30}, GS_{60}, and GS_{90} indicate 0, 30, 60, 90 Mg ha^{-1} of granulated straw incorporation, respectively. Lowercase letters indicate significant differences at P<0.05 among treatments in upland or paddy soil by ANOVA for randomized complete block design and Tukey's post hoc test. Asterisks (*) indicate significant differences at P<0.05 between upland and paddy soils for the same treatment assessed by the independent-sample t-test.

(Fig. 2-A and B). Similar patterns of V-, S-, and C-type phenols were observed in both upland and paddy soils (Fig. 2-A and B).

In upland soil, the total amino sugars content increased by 39.7, 85.2 and 227.0 mg kg^{-1} (equivalent to 14.9, 32.1 and 85.6%) compared to control with increasing straw incorporation (Fig. 3-A). A similar increasing trend was observed for F-GlcN, while MurN showed a steady increase of 7.0, 9.5 and 12.6 mg kg^{-1} (equivalent to 85.9, 117.1 and 158.3%) (Fig. 3-A and B). In paddy soils, the incorporation of granulated straw at 30, 60, and 90 Mg ha^{-1} resulted in comparable increases in total amino sugars, F-GlcN, and MurN (Fig. 3-A–C). In both soil types, straw incorporation did not alter the ratios of F-GlcN/MurN.

Notably, no significant differences in the ratios of amino sugars to SOC among treatments were observed in either upland or paddy soil, with higher values for the former, except for the 30 Mg ha^{-1} treatment (Fig. 4-A). With increasing incorporation, the ratios of lignin phenols to SOC increased by 3.8, 64.7, and 151.0% in upland, and by 292.2, 278.4, and 462.3% in paddy soil, respectively (Fig. 4-B). As straw amounts increased, the ratio of lignin phenols to amino sugars increased by 12.0, 15.4, and 36.1% in upland, and by 14.4, 35.1, and 63.9% in paddy, respectively (Fig. 4-C).

3.3. Microbial PLFAs and community composition

At the earlier stage (day 30), with increasing levels of straw incorporation, the total microbial PLFAs increased by 39.4, 69.4, 177.6% in upland, and by 29.1, 48.1, 48.4% in paddy compared to their respective controls (Fig. 5-C). Correspondingly, the MBC content increased by 64.1, 270.1, 412.0% in upland, and by 18.9, 52.5, 70.8% in paddy (Fig. 5-D). Additionally, the ratios of fungi/bacteria and $Gram^{-}/Gram^{+}$ increased distinctly with granulated straw incorporation, particularly in upland soil (Fig. 5-E). Subsequently, these increasing trends gradually diminished over the one-year observation period.

Granulated straw incorporation at varying amounts led to a comparable increase in both abundance-based coverage estimator (ACE) index and Shannon-Wiener diversity index (Shannon) of soil bacterial communities in upland soil, whereas no significant differences were detected in paddy soil (Fig. 6-A and B). Higher levels of straw incorporation reduced both ACE index and Shannon diversity of fungi in both soils, but only decreased ACE index in paddy soil. At the class level, straw incorporation increased the abundance of Gammaproteobacteria in both soils, but decreased Alphaproteobacteria in upland and Anaerolineae in paddy soil (Fig. 6-C). With increasing straw incorporation, the abundance of Sordariomycetes decreased in upland soil, but increased in paddy soil (Fig. 6-D–F).

The ACE index and Shannon diversity of bacteria in paddy soil exceeded those in upland soil under control conditions, while no significant differences emerged among treatments with straw incorporation (Fig. 6-A and B). Fungal Shannon diversity was higher in upland soil compared to paddy soil, whereas the ACE index demonstrated an inverse pattern (Fig. 6-D and E). Upland soils exhibited higher abundances of Alphaproteobacteria, Vicinamibacteria, Sordariomycetes, and Agaricomycetes relative to paddy soils (Fig. 6-D and E).

3.4. Relationships between microbial traits and SOC accumulation

In both upland and paddy soils, lignin phenols to SOC ratios demonstrated negative correlations with Actinomycetes

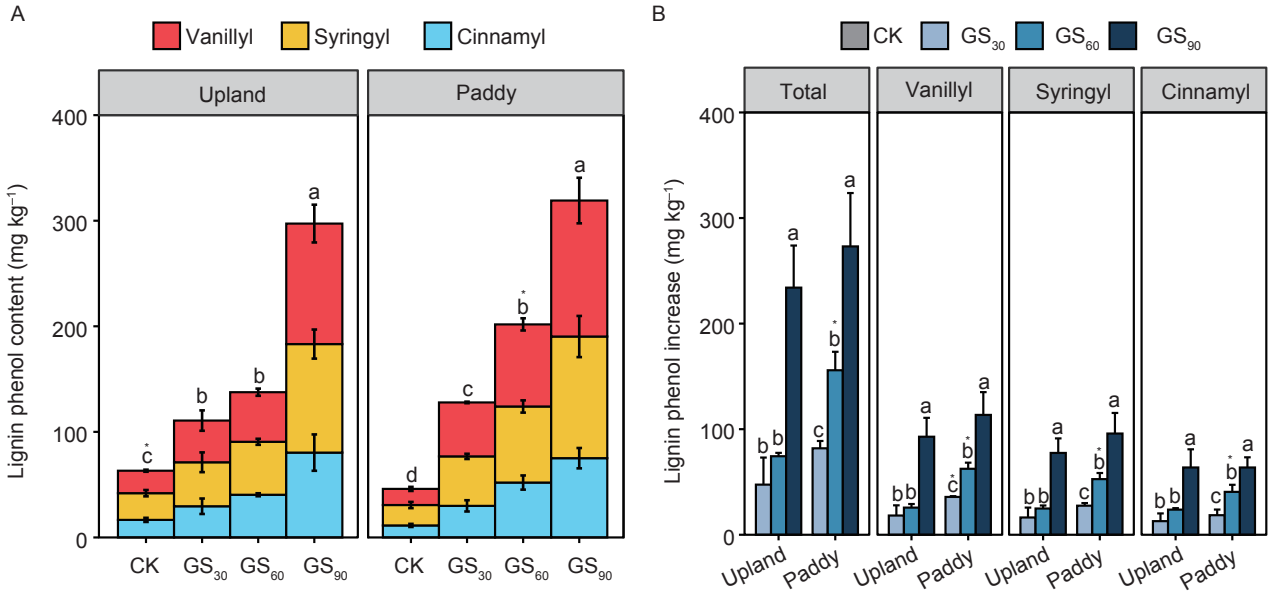


Fig. 2 The concentrations (A) and increments (B) of lignin phenols (vanillyl-, syringyl- and cinnamyl-phenols) in infertile upland and paddy soils following granulated straw incorporation after one year. CK, GS_{30}, GS_{60}, and GS_{90} indicate 0, 30, 60, 90 Mg ha^{-1} of granulated straw incorporation, respectively. Lowercase letters indicate significant differences at $P<0.05$ among treatments in upland or paddy soil by ANOVA for randomized complete block design and Tukey's post hoc test. Asterisks (*) indicate significant differences at $P<0.05$ between upland and paddy soils for the same treatment assessed by the independent-sample *t*-test.

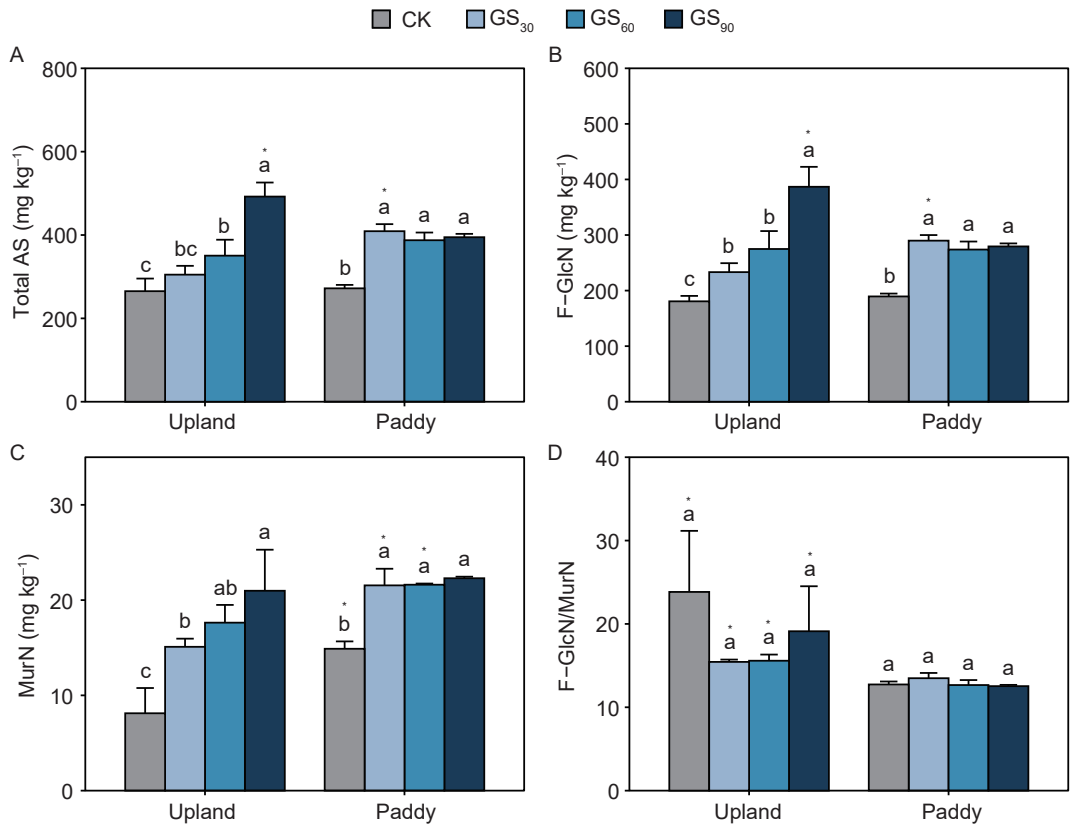


Fig. 3 Contents of total amino sugars (AS; A), fungal-derived glucosamine (F-GlcN; B), muramic acid (MurN; C), and the ratios of F-GlcN/MurN (D) in infertile upland and paddy soils following one year of granulated straw incorporation. CK, GS_{30}, GS_{60}, and GS_{90} indicate 0, 30, 60, 90 Mg ha^{-1} of granulated straw incorporation, respectively. Lowercase letters indicate significant differences at P<0.05 among treatments in upland or paddy soil by ANOVA for randomized complete block design and Tukey's post hoc test. Asterisks (*) indicate significant differences at P<0.05 between upland and paddy soils for identical treatments assessed by the independent-sample t-test.

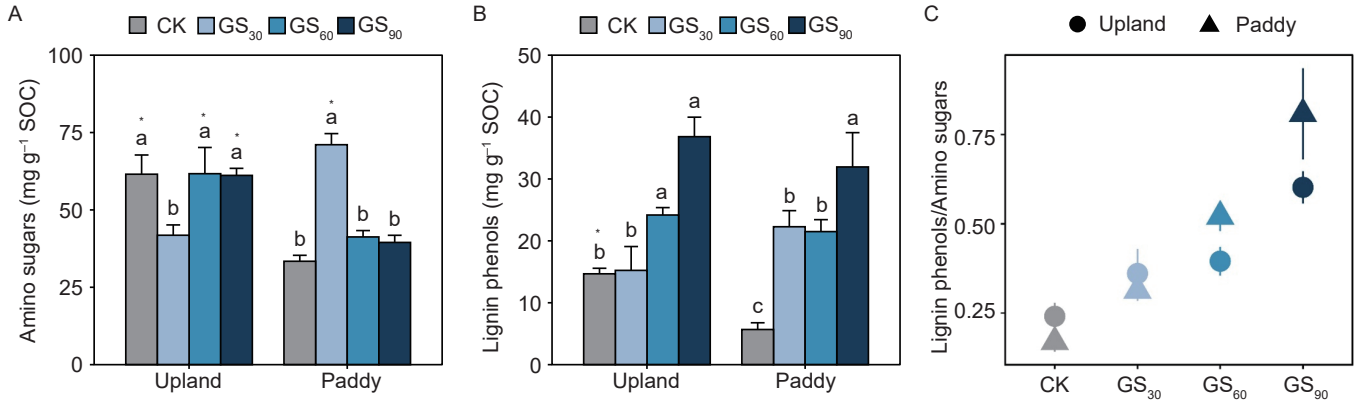


Fig. 4 Concentrations of amino sugars (A) and lignin phenols (B) within soil organic carbon (SOC), and the corresponding ratios of amino sugars to lignin phenols (C) in upland and paddy soils following one year of granulated straw incorporation. CK, GS_{30}, GS_{60}, and GS_{90} indicate 0, 30, 60, 90 Mg ha^{-1} of granulated straw incorporation, respectively. Lowercase letters indicate significant differences at P<0.05 among treatments in upland or paddy soil, determined by ANOVA for randomized complete block design and Tukey's post hoc test. Asterisks (*) indicate significant differences at P<0.05 between upland and paddy soils for identical treatments, assessed *via* independent-sample t-test.

abundance but positive correlations with the Gram$^-$/Gram$^+$ ratio. In upland soil specifically, the lignin phenol to SOC ratios showed positive associations with fungal abundance and the fungi/bacteria ratio, while exhibiting negative correlations with the fungal ACE index (Fig. 7-A–F).

In upland soil, amino sugars and F-GlcN to SOC ratios correlated negatively with the fungal ACE index, while the MurN to SOC ratio displayed a negative relationship with fungal Shannon diversity (Appendix C). The analysis revealed no significant correlations between amino sugars to SOC ratios

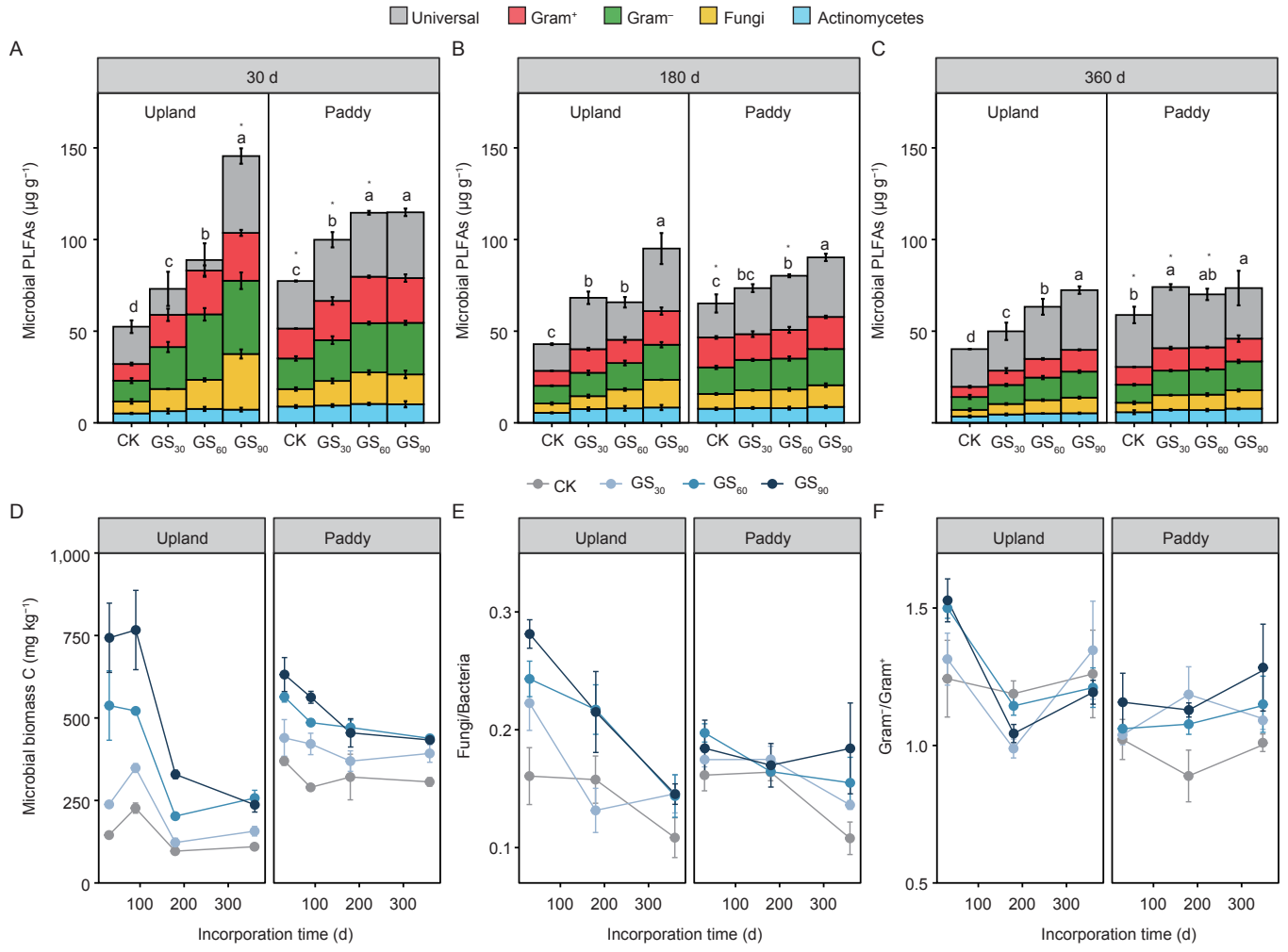


Fig. 5 Microbial PLFA content in infertile upland and paddy soils at 30, 180, and 360 days following granulated straw incorporation (A–C), and the temporal changes in microbial biomass C (D) and the ratios of fungi to bacteria (E) and Gram$^+$ to Gram$^-$ bacteria (F) following granulated straw incorporation in infertile upland and paddy soils. CK, GS_{30}, GS_{60}, and GS_{90} indicate 0, 30, 60, 90 Mg ha^{-1} of granulated straw incorporation, respectively. Lowercase letters indicate significant differences at $P<0.05$ among treatments in upland or paddy soil using ANOVA for randomized complete block design and Tukey's post hoc test. Asterisks (*) indicate significant differences at $P<0.05$ between upland and paddy soils for identical treatments, assessed by independent-sample *t*-test.

and microbial individual percentages (Appendix C).

4. Discussion

4.1. Efficiency and patterns of SOC accumulation with increasing granulated straw incorporation

One year after granulated straw incorporation, SOC accumulation efficiency ranged from 30.8–37.5% in upland and from 38.3–60.0% in paddy (Fig. 1-C), surpassing traditional practices with chopped crop straw incorporation (5.7–20.5% (Lu 2015; Wang *et al.* 2019, 2021; Berhane *et al.* 2020; Li *et al.* 2023). This innovative practice of granulated crop straw incorporation into the plough layer substantially enhances soil C retention efficiency. The higher SOC accumulation efficiency in paddy compared to upland with straw input (Fig. 1-C) indicates that granulated straw incorporation more effectively improves straw-C retention efficiency in paddy soil. Granulated straw incorporation yielded lower SOC accumulation efficiency in subtropical uplands (30.8–37.5%) compared to mid temperate regions (45.7%) as reported by Cong *et al.* (2020). This observation suggests that high temperature and humidity conditions reduce straw-C retention efficiency, even with granulated straw incorporation. The present study demonstrates significant improvements in crop yield and SOC content in both upland and paddy soils through single incorporation of substantial granulated crop straw (Table 1; Fig. 1). With increasing straw incorporation, SOC accumulation efficiency remained constant in upland but decreased significantly in paddy (Fig. 1-C), partially contradicting our first hypothesis. This suggests that upland soil remains far from C saturation, while paddy soil approaches C saturation (Six *et al.* 2002; Stewart *et al.* 2007).

Upland and paddy soils exhibited similar patterns of lignin phenol increase with increasing straw incorporation, showing synchronized increases in three lignin monomer types (Fig. 2). Typically, V- and S-type phenols accumulate preferentially compared to C-type in soils, as C-type phenols in the outermost cell wall layer are more accessible to

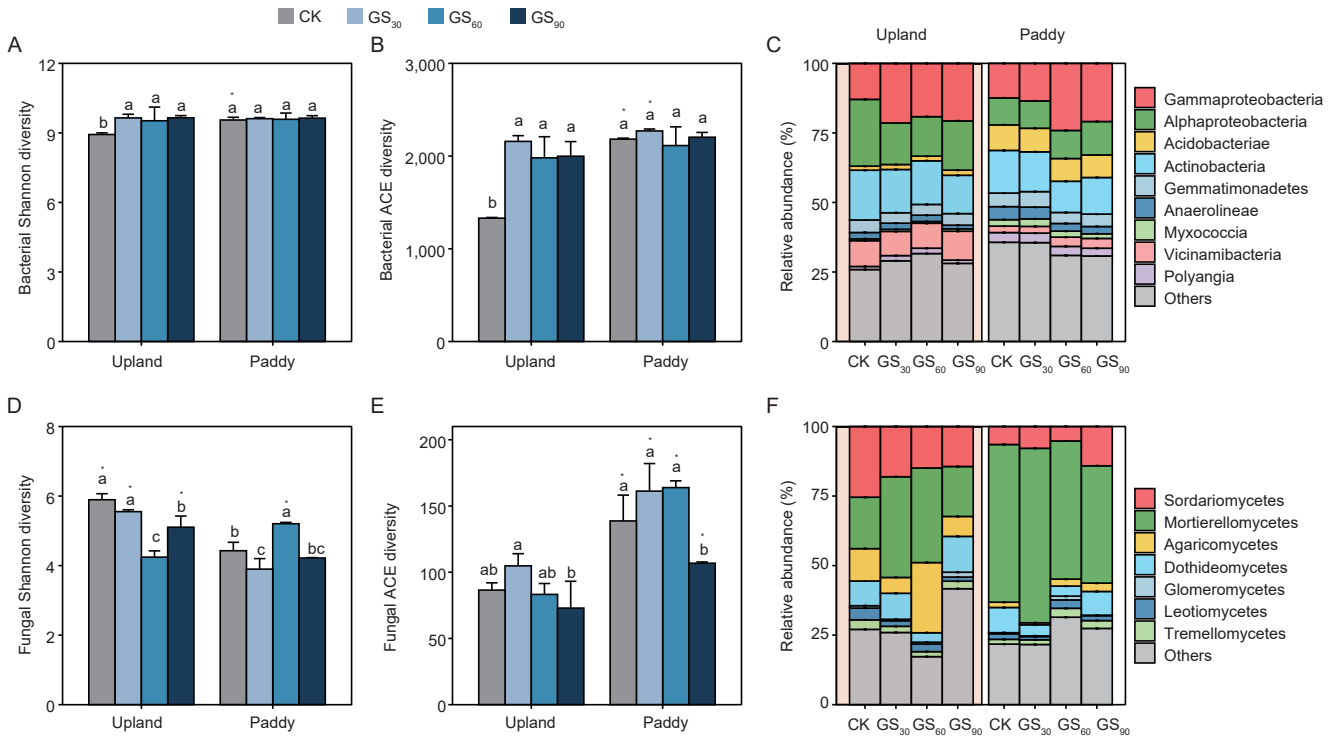


Fig. 6 The Shannon-Wiener and abundance-based coverage estimator (ACE) diversity indices of bacteria (A and B) and fungi (D and E), and the relative abundance of taxonomic groups at class level (C and F) following an one-year period of granulated straw incorporation. CK, GS_{30}, GS_{60}, and GS_{90} indicate 0, 30, 60, 90 Mg ha^{-1} of granulated straw incorporation, respectively. Lowercase letters indicate significant differences at $P<0.05$ among treatments in upland or paddy soil, determined by one-way ANOVA and Tukey's post hoc test. Asterisks (*) indicate significant differences at $P<0.05$ between upland and paddy soils for identical treatments, assessed by the independent-sample *t*-test.

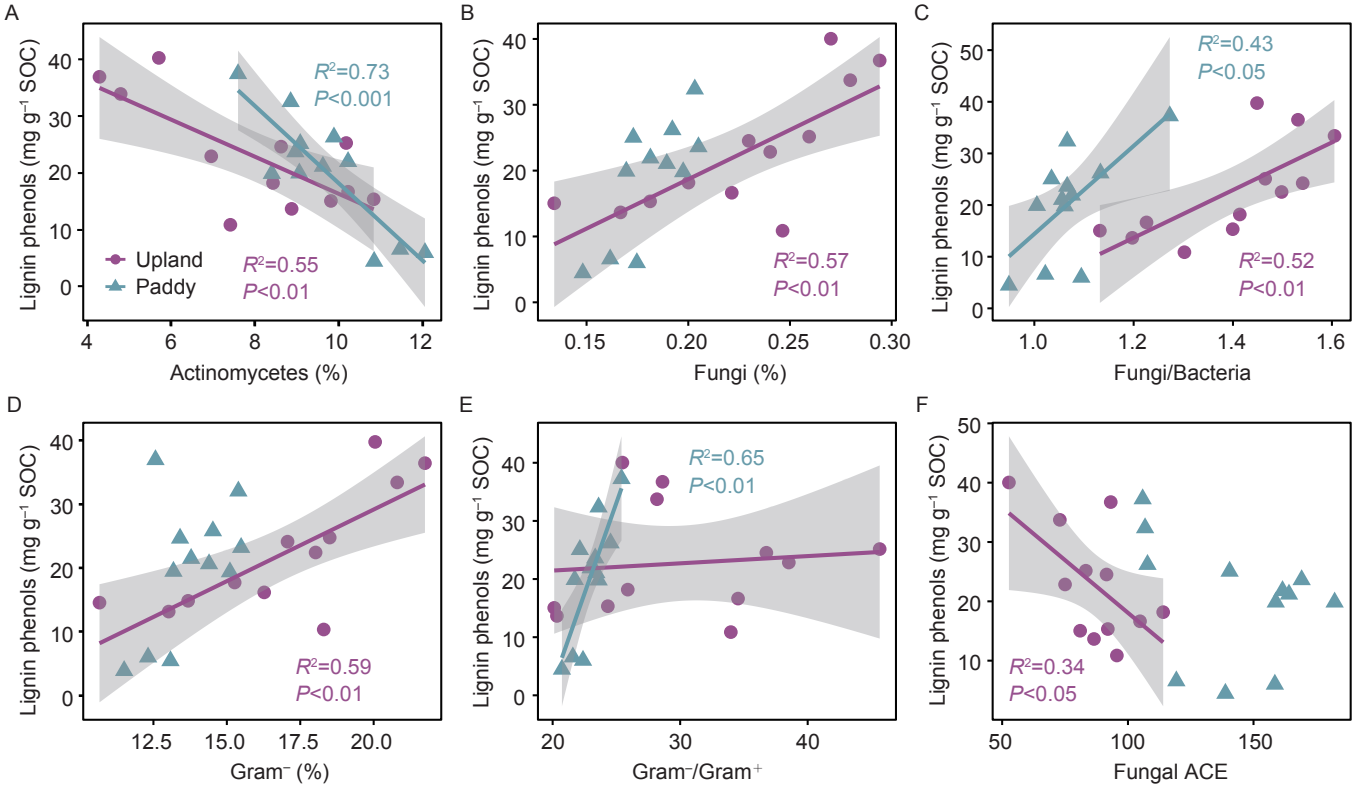


Fig. 7 Linear regression analysis of lignin phenols in soil organic carbon (SOC) relative to microbial traits. ACE, abundance-based coverage estimator. Rose red circles indicate upland soil samples, while dusty blue triangles represent paddy soil samples.

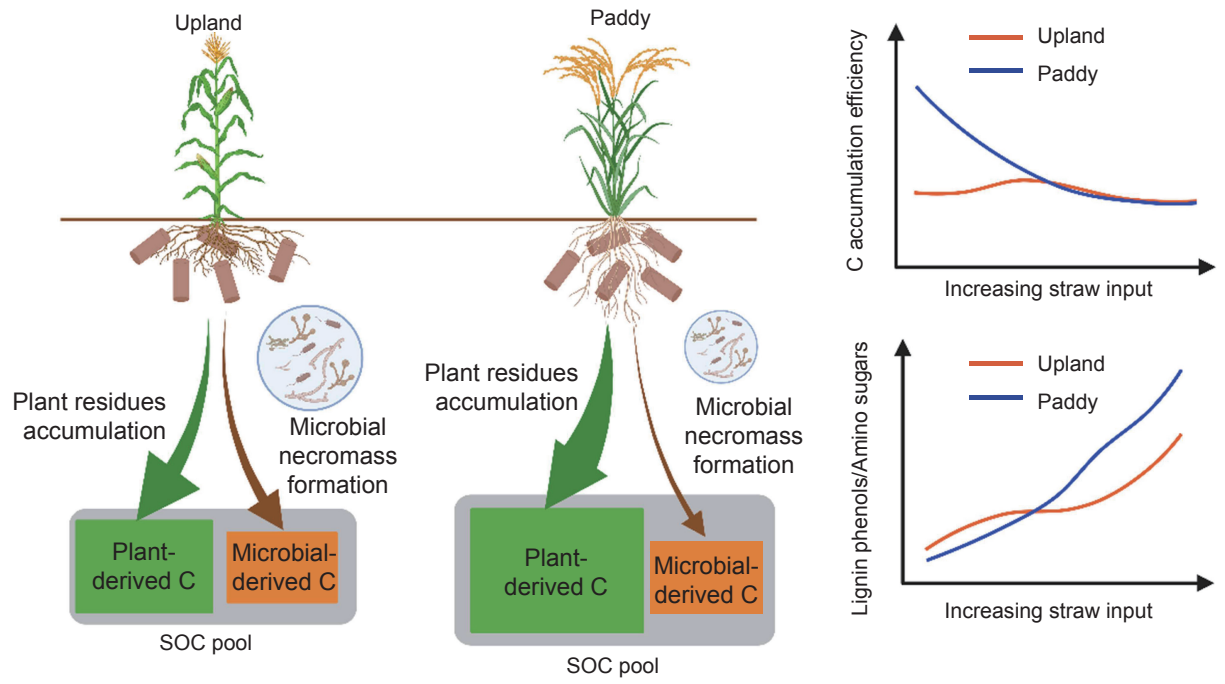


Fig. 8 The diagram depicts the process of new soil organic carbon (SOC) formation in upland and paddy soils following granulated straw incorporation. Green and brown arrows indicate the pathways of plant residue and microbial necromass accumulation, respectively. The arrow width represents the intensity of these pathways. In both soil types, the newly incorporated straw primarily accumulates as plant residues, with particularly high accumulation in paddy soil. As granulated straw input increases, SOC accumulation efficiency maintains stability in upland soil while showing progressive decline in paddy soil. The ratios of lignin phenols to amino sugars demonstrate a gradual increase corresponding to higher straw input levels.

microorganisms (Chen *et al.* 2018a; Kösters *et al.* 2018). In this study, the granulation process likely disrupted the crop straw's epidermal tissue and vascular bundles, leading to non-selective microbial decomposition of lignin phenols (Bahri *et al.* 2006). Upland and paddy soils had contrasting amino sugar accumulation patterns (Fig. 3-A). In upland soil, amino sugar contents and their fungal and bacterial biomarkers increased proportionally with straw input, while these parameters remained unchanged across the three straw input levels in paddy soil (Fig. 3-B and C). This short-term experimental result aligns with observations that long-term SOC accumulation in paddy soil primarily derives from plant-derived C (Chen *et al.* 2021). These findings indicate that while granulated straw incorporation promotes similar lignin preservation in both soil types, it results in different microbial necromass accumulation patterns due to distinct soil environments.

The ratio of lignin phenols to amino sugars increased almost linearly with increasing straw incorporation, indicating that the C increment in bulk soils originates more from plant residues than microbial necromass (Figs. 4-C and 8). This suggests reduced microbial uptake and catabolism of newly input C, as straw granulation limits soil microbes' attachment to straw particles through spatial isolation (Zhang *et al.* 2018). This inhibition of microbial C metabolism is more pronounced in paddy than in upland soil (Duan *et al.* 2024b). Evidence includes the lesser increase in living microbial biomass (PLFAs, MBC) and absence of increase in microbial necromass with increasing straw input in paddy (Figs. 3 and 5). This may be attributed to periodic higher soil moisture conditions in paddy soil reducing microbial activity (Qiu *et al.* 2018; Deng *et al.* 2021), thereby inhibiting microbial necromass production. Notably, the magnitude of lignin phenols increment exceeds that of amino sugars and total SOC pools with granulated crop straw incorporation (Fig. 4-B). Given the challenges of SOC promotion in subtropical regions with high temperature and humidity (Tang *et al.* 2024), incorporating granulated crop straw into the plough soil layer presents an innovative and effective approach to rapidly enhance SOC in infertile croplands, particularly in the form of plant residues. These findings demonstrate the potential of granulated straw incorporation as an effective strategy for increasing SOC storage in subtropical infertile croplands.

4.2. SOC accumulation patterns in relation to microbial traits

Both upland and paddy soils demonstrated an increasing contribution of plant residues to SOC with higher levels of granulated straw incorporation (Figs. 4 and 8), indicating an inhibition of lignin phenols decomposition as evidenced by the increasing acid-to-aldehyde ratio of lignin (Appendix D). This phenomenon partially results from the decreased abundance of Actinomycetes and increased abundance of Gram$^-$ bacteria (Figs. 5 and 7; Appendix E). Research has shown that Actinomycetes effectively survive and decompose lignin compounds under moderate organic materials conditions (Li *et al.* 2014; Janusz *et al.* 2017), while massive straw incorporation inhibits Actinomycetes growth

(Appendix E). Conversely, the increased proportion of $Gram^-$ bacteria intensifies the inhibition of lignin decomposition, as these bacteria preferentially utilize labile organic substrates over recalcitrant lignin compounds (Derrien *et al.* 2014; Li *et al.* 2022). These microbial community shifts indicate that substantial granulated straw incorporation modifies the decomposer community structure, promoting plant-derived C stabilization in soil.

The well-drained upland soil, compared to moist-irrigated paddy, exhibited stronger correlations between lignin phenols and amino sugars in SOC to microbial traits (Appendix C). This indicates enhanced microbial involvement during straw C transformation due to well-drained soil conditions, even with granulated straw particles (Chen *et al.* 2021; Duan *et al.* 2024a). The bacterial necromass contribution to SOC accumulation in upland soil relates to higher abundance and diversity of $Gram^-$ and $Gram^+$ bacteria (Appendices C and E). $Gram^+$ bacteria possess thicker peptidoglycan cell walls, rendering their necromass more chemically resistant and persistent in soil, thus contributing more substantially to long-term SOC storage (Hawkes *et al.* 2017). $Gram^-$ bacteria rapidly proliferate and contribute significant microbial biomass under favorable conditions, supporting short-term necromass formation (Meisner *et al.* 2013; Canarini *et al.* 2017). Furthermore, increased bacterial diversity enhances the microbial community's metabolic capabilities, enabling more efficient decomposition of diverse straw components, resulting in greater microbial necromass production and incorporation into SOC pool (Zhang *et al.* 2023). The fungal necromass contribution to SOC accumulation in upland appears primarily influenced by fungal biomass rather than community diversity. This suggests fungal growth's predominant role in necromass formation under massive granulated straw conditions. Higher fungal biomass indicates greater production of cell wall materials such as chitin and melanin, which are chemically recalcitrant and significantly contribute to long-term SOC accumulation (Khan *et al.* 2016; Liu *et al.* 2019).

4.3. Implications for rapid amelioration of infertile croplands

This study demonstrated that granulated straw incorporation rapidly enhanced both crop yield and SOC pools in subtropical upland and paddy (Table 1; Fig. 1). However, this innovative approach is applicable only under specific conditions. The massive incorporation of granulated crop straw into the plough layer proves unsuitable for flooding conditions in paddy fields, as evidenced by preliminary experiments (Appendix F). Rice root development was significantly impaired due to reducing substances generated during anaerobic decomposition of straw (Wang *et al.* 2020; Li *et al.* 2024). Furthermore, the process generated substantial greenhouse gas emissions (CH_4) from flooding paddy, even with lower levels of granulated straw incorporation (30 Mg ha^{-1}) (Appendix F). Therefore, dry-rice cultivation with moist-irrigation is recommended for infertile paddy during the amelioration phase.

In both upland and paddy conditions, single incorporation of 90 Mg ha^{-1} granulated straw did not achieve maximum SOC accumulation, particularly in the form of plant residues (Fig. 1). The optimal dosages of granulated straw incorporation differed between upland and paddy fields when considering SOC accumulation efficiency and crop yield. These parameters exhibited distinct responses to varying levels of granulated straw input. In upland conditions, SOC accumulation efficiency remained constant with 30–90 Mg ha^{-1} straw input, while crop yield plateaued beyond 60 Mg ha^{-1} (Table 1; Fig. 1). In paddy conditions, SOC accumulation efficiency decreased markedly from 30 to 90 Mg ha^{-1} straw input, accompanied by minimal yield increases (Table 1; Fig. 1). Given the abundant organic resources from rice straw in subtropical double rice cropping systems, incorporating this straw into infertile croplands through granulation presents a viable approach for enhancing crop yield and soil quality.

5. Conclusion

Increasing the SOC pool remains challenging in subtropical croplands due to intense microbial catabolism of organic materials in regions characterized by high temperature and humidity. This study demonstrates that massive incorporation of granulated crop straw effectively enhances both crop yields and SOC levels in infertile upland and paddy soils over the short term. The SOC increases in both croplands are predominantly attributed to plant residues rather than microbial necromass with increasing granulated straw incorporation. These results indicate that granulating crop straw may reduce microbial participation in straw decomposition, thereby promoting SOC accumulation primarily as plant residues. However, the plant residue-derived C from straw in soil will inevitably undergo gradual decomposition and loss under southern China's climatic conditions over the long term. Consequently, enhancing the stability of retained straw-derived C requires further investigation.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used ChatGPT web version to assist in improving the clarity and readability of the language. All content generated was carefully reviewed and revised by the authors as necessary, and the authors take full responsibility for the final content of the article.

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