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No-tillage practice enhances soil total carbon content in a sandy *Cyperus esculentus* L. field

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Abstract

Background No-tillage (NT) is a widely used field management to reduce soil erosion and degradation and is suggested to be beneficial for enhancing soil carbon (C) sequestration capacity. Nonetheless, the effects of NT on soil total carbon (TC) content in aeolian sandy soils are not extensively explored, and the underlying mechanisms are not clear. In our field experiments, the influence of NT and conventional tillage (CT) on sandy soil was studied.

Methods We estimated the changes in soil TC in response to NT practice in a *Cyperus esculentus* L. field located at semi-arid Horqin sandy land, China. To unravel the underlying mechanisms, plant traits, soil properties and soil microbial characteristics were measured in parallel. The variations in soil bacterial community structure were investigated by 16S rRNA amplicon sequencing. The functionality of soil bacterial community was predicted based on OTU tables by using PICRUSt2.

Results NT increased soil TC content in this sandy agroecosystem within a short-term experimental period, compared to CT. The underlying mechanisms might rely on three aspects. First, NT increased soil TC content through increasing photosynthesis and plant biomass, and thus, the plant-derived dissolved organic C. Second, NT increased the C immobilized in soil microbial biomass by increasing microbial C demands and C use efficiency. Third, NT increased the dominance of oligotrophic members in bacterial communities by decreasing available nutrient levels, which is associated with the recalcitrance and stability of the soil organic carbon.

Conclusions The present study enriched our knowledge on the changes in the plant-soil-microbe continuum in response to NT in a semi-arid sandy agroecosystem. Still, this study provides a reference for modifying tillage practices to benefit crop yield as well as soil C sequestration.

Keywords No-tillage, Bacterial community composition, Bacterial function prediction, Aeolian sandy soil, *Cyperus esculentus* L.

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Background

No-tillage (NT) practice is a widely utilized conservation tillage management to reduce agricultural soil erosion and degradation (Lal 2004; Montgomery 2007). Compared to conventional tillage (CT), NT is recommended as an efficient management strategy that can improve soil aggregation (Six et al. 2000; Wang et al. 2019), decrease soil organic carbon (SOC) decomposition (Leite et al. 2004; Zheng et al. 2023), and thus enhance soil carbon (C) sequestration (Lal 2004). However, most of the findings were obtained from loamy soils. In arid and semi-arid sandy agroecosystems, the impacts of NT practice on the soil total carbon (TC) content are not completely explicated. Elucidating the impacts of NT practice on the soil TC and the underlying driving mechanisms in sandy agroecosystems would be helpful for predicting the C budget in desertification farmlands, providing guidelines for designing optimal tillage management that mitigates soil erosion and maintains high soil C storage.

The consequences of NT practice on soil TC content might be driven by a series of complicated mechanisms. A number of studies reported that, compared to CT practice, NT practice can directly increase the soil TC content by increasing the supply of plant-derived C (Gale and Cambardella 2000; Crow et al. 2018; Vezzani et al. 2018; Gao et al. 2021; Tian et al. 2024). NT usually increased crop photosynthesis (Du et al. 2020) and increased the belowground allocation of photosynthesized C (Niu et al. 2019). On one hand, NT can improve soil structure and increase moisture retention capacity, providing an optimal condition for crop root growth. The increased photosynthesized C increases the root length and biomass density in the upper layers, which subsequently increase root residues (Zhu et al. 2022; Yin et al. 2024). The increased root residues could enhance SOC through both the "dissolved organic carbon (DOC)-microbial" path and the "physical transfer" path, thereby augmenting soil TC content (Yang et al. 2023). On the other aspect, the increased belowground allocation of photosynthesized C can increase rhizodeposits (Ge et al. 2012). Rhizodeposits have an immediate enhancing effect on active organic C fractions, such as dissolved organic matter (DOC), and can enter the soil SOC pool through microbial transformation (Li et al. 2023).

NT practice can also influence the soil C storage by changing soil microbial community metabolism. Microbial C use efficiency (CUE) represents the ratio of growth over C uptake (Manzoni et al. 2012), and thus, high microbial CUE typically implies great C sequestration potential (Tao et al. 2023). It was proposed that CT practice decreased microbial CUE, while NT practice can increase SOC sequestration through increasing microbial CUE (Zhang et al. 2022). Under the oxygen-limited conditions of NT management, less SOC is lost as microbial respiration and a higher proportion of available C was concerted into the microbial biomass. Still, NT practice typically enhanced the N and P availability of surface soils. To maintain stoichiometric homeostasis, soil microorganisms would increase C demand, and consequently improve their CUE (Song et al. 2022).

Beyond microbial CUE, NT practice might influence soil TC content by altering soil microbial community composition, and thus the trophic cascade. Phospholipid fatty acid (PLFA) based measurement of microbial community composition revealed that the abundance of Gram-positive(G+) bacteria increased, while Gram-negative (G−) decreased under NT practice compared to CT (Rahman et al. 2008; Bai et al. 2016). Using 16S rRNA amplicon sequencing method, it was found that the relative abundance of Acidobacteria and Chloroflexi increased during the implementation of NT, whereas bacterial taxa of Proteobacteria, Firmicutes, and Bacteroidetes decreased in proportion (Li et al. 2020; Pathan et al. 2021; Araujo et al. 2023). All these findings indicated a shift towards a dominance of oligotrophic members in microbial communities under NT treatment, since G+bacteria are usually considered as oligotrophic members in comparison with G-; and at the finer taxonomic resolution, the members of Proteobacteria and Acidobacteria are classified as representatives of copiotrophic and oligotrophic bacteria, respectively (Fierer et al. 2007; Li et al. 2021). Since the oligotrophic members typically reside in habitats with more recalcitrant and complex C components, the enrichment of oligotrophic taxa indicates an increase of recalcitrant and stable SOM under NT practice, which subsequently alleviates the loss of soil C (Li et al. 2021).

In the present study, two treatments of conventional tillage (CT) and no-tillage (NT) were implemented in a *Cyperus esculentus* field, which located in the erosion-prone region of the southern Horqin sandy land, China. Soil TC content, plant physiological traits, soil N and P nutrients, microbial biomass and enzymatic activities, and soil bacterial community composition and potential ecological functions under two contrasting tillage regimes were examined, aiming to investigate the impacts of NT practice on soil TC content in this semi-arid sandy agroecosystem and unravel the underlying mechanisms. We hypothesize that, in comparison with CT, planting *C. esculentus* with NT practice would increase soil TC content by (1) enhancing the plant photosynthesis and biomass, thereby increasing plant-derived dissolved C; (2) increasing microbial C demands and consequently enhancing soil microbial CUE; (3) promoting the prevalence of oligotrophic members in bacterial communities and thus mitigating the mineralization of SOC.

Materials and methods

Site description and experimental design

A field experiment was established in 2020 in a desertified farmland of the southeastern portion of the Horqin sandy land, Zhangwu County, Liaoning Province, China (42.58°N, 122.67°E). This region has a temperate continental semiarid monsoon climate, with mean annual precipitation of 450–550 mm, mean annual evaporation of 1200–1450 mm, and mean annual temperature of 5.7 °C. The experimental site is intensively subjected to aeolian actions manifested by frequent occurrences of sand and dust storms in spring, with an average annual wind speed of 3.0 m s^{-1} and a maximum wind speed of 27.1 m s^{-1}. The soil is classified as Arenosols according to World Reference Base for Soil Resources (WRB) classification system, with bulk density of 1.63 g cm^{-3} and organic matter content of 2.62 g kg^{-1} (topsoil 0–20 cm) (Li et al. 2019). Soil texture of the experimental site is sandy soil with 99.32% sand, 0.45% silt, and 0.23% clay.

The planted crop, *Cyperus esculentus* L. (tiger nut or chufa), is an edible perennial C_4 plant from the sedge family (Cyperaceae). It is well-suited for cultivation in arid and nutrient-deficient regions (Bai et al. 2021), owing to its strong drought tolerance, tillering ability, and well-developed root system (Asare et al. 2020; Cheng et al. 2020). Two soil management practices, conventional tillage (CT) and no-tillage (NT), were set. Each treatment was replicated in three 7 m×7 m experimental plots with a 2 m buffer zone. CT was mouldboard ploughed to a depth of 20 cm to loosen the topsoil and prepare the seedbed. The ridges were 45 cm wide and 25 cm high, as commonly practiced in the experimental region. In contrast, NT plots were manipulated following a standardized NT protocol, leaving soil undisturbed throughout the experimental period except for planting (Derpsch et al. 2014). The nitrogen, phosphorus, and potassium fertilizers were urea, diammonium phosphate and potassium sulfate, respectively. These were applied as basal fertilizers at rates of 326.53 kg N ha^{-1} $year^{-1}$, 170.36 kg P_2O_5 ha^{-1} $year^{-1}$, and 212.95 kg K_2O ha^{-1} $year^{-1}$. For CT, seeds were planted into ridges, and the basal fertilizer was applied in the plow furrow before sowing. NT plots were directly sown to a depth of 10–12 cm with furrow opener. Seeds and fertilizer were placed in the same row with 45 cm row spacing. *C. esculentus* seeds were hand-planted uniformly according to traditional farmers' practices with a seeding rate of 300 kg ha^{-1} and 15 cm seed spacing on June 10 and harvested on October 11.

Plant sampling and traits analysis

At the peak of growing season, the upper mature, fully expanded leaves of *C. esculentus* from each plot were used for gas exchange measurements. A portable gas exchange system (Li-6400, Li-COR Inc., Lincoln, NE, USA) was used for gas analysis. Measurements were taken from 9 a.m. to 11 a.m. when the site was sunlit. The value of photosynthetically active radiation (PAR) value was set at 1000 μmol m^{-2} s^{-1}, controlled by a red-blue light source. The parameters directly measured by Li-6400 included net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (T_r). Following the P_n measurements, the selected leaves were picked and immediately immersed in liquid nitrogen for subsequent analysis of soluble protein content. The soluble protein content of *C. esculentus* leaves was determined using the Coomassie Blue-G dye-binding method (Read and Northcote 1981).

After measuring the gas exchange parameters, plant roots were sampled by collecting a 50×50×50 cm soil block from each plot using a steel plate and a shovel. The soil blocks were then gently loosened by hand to separate the roots from the soil. The separated plant roots were carefully washed to remove any adhering soil and placed in iceboxes for transportation to the laboratory. Before determining the root morphological traits, all root samples were frozen at – 20 °C. Within each plot, at least 10 intact individual plants of *C. esculentus* were used to determine the root morphological traits. The average root diameter, total root length, and surface area were determined using scanned images processed by WinRHIZO software (Regent Instruments Inc., Québec City, Quebec, Canada). We then calculated root diameter (mm), specific root length (SRL, root length per unit dry weight, m g^{-1}), specific surface area (SSA, root surface area per unit dry weight, cm^2 g^{-1}).

Aboveground biomass was sampled by clipping all individuals to soil surface within a randomly selected 1 m×1 m plot in each treatment area. Root and tuber biomass were collected from the 0–50 cm of soil in the selected 1 m×1 m plot. All the above samples were then dried at 65 °C for 72 h until a constant weight was achieved.

Soil sampling and properties analysis

Soil samples were collected after clipping the aboveground biomass. For each plot, five cores of topsoil (0–15 cm depth) were randomly collected using a 5-cm diameter auger and were homogenized into one composite sample. The collected soils were sieved through a 2-mm sieve to remove visible roots, plant residues, and stones, and were then transferred to the laboratory in sterile sample bags. All soil samples were divided into three subsamples: (i) one was stored at 4 °C for measuring soil ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N), dissolved organic carbon (DOC),

activities of soil enzymes involved in C, N cycles, soil microbial biomass carbon and nitrogen (MBC, MBN), and soil respiration, (ii) one was stored at − 20 °C for microbial community analysis, and (iii) the remaining samples were air-dried for analysis of soil total carbon (TC), soil total nitrogen (TN), plant readily available phosphorus (Olsen P).

Soil TC and TN were determined using an elemental analyzer (Elementar Analysensysteme Vario MACRO cube, Germany). DOC was extracted by 0.5 M potassium sulfate (K_2SO_4) (2:1, v/w, solution: soil) and quantified using a total organic carbon (TOC) analyzer (HT1300, Analytikjena, Jena, Germany). Soil Olsen P was extracted with 0.5 M $NaHCO_3$ (pH 8.5, 10:1, v/w solution:soil) (Olsen et al. 1954) and quantified by molybdenum blue colorimetric at 880 nm wavelength (Murphy and Riley 1962). NH_4^+-N and NO_3^--N were extracted by 2 M KCl (5:1, v/w, solution:soil) and quantified using an autoAnalyser III continuous Flow Analyzer (AA3, Bran Luebbe, Norderstedt, Germany).

The soil MBC and MBN were determined using the chloroform ($CHCl_3$) fumigation-extraction method within 7 days after soil sampling (Vance et al. 1987). The activities of β-1,4-glucosidase (BG) and N-acetyl-β-D-glucosaminidase (NAG) were determined according to Bottomley et al. (1994). Soil respiration was calculated based on the gas flow rate (GFM 17, Aalborg, USA) and the headspace CO_2 content (Li-820, Li-COR Inc., Lincoln, NE, USA) in flasks after incubation at 25 °C. Soil basal respiration (BR) was determined as described in Li et al. (2021). Additionally, a 2 ml 6% glucose solution was evenly added to the soil sample and allowed to react for 1.5 h to measure the substrate-induced respiration (SIR). The soil microbial C limitation index (CLI), representing C starvation status for microbes and indicating high C demands, was calculated as SIR/BR (Hou et al. 2019). The metabolic quotient (qCO_2), representing the respiration rate per unit microbial biomass, was calculated as BR/MBC (Zuber and Villamil 2016). The microbial CUE was calculated based on C:N stoichiometry as follows:

$$CUE = CUE_{max}[S_{C:N}/(S_{C:N} + K_N)] \quad (1)$$

$$S_{C:N} = (1/E_{C:N}) \times (B_{C:N}/L_{C:N}) \quad (2)$$

where CUE represents the microbial C use efficiency. $S_{C:N}$ is a scalar that represents the extent to which the allocation of enzyme activities offsets the disparity between the ratios of available resources and microbial biomass. K_N is the half-saturation constant set to 0.5. CUE_{max} is the upper limit for microbial growth efficiency set to 0.6 based on thermodynamic constraints. $E_{C:N}$ represents the ratio of enzyme activities directed toward acquiring C and N from the environment, calculated as BG/NAG. $L_{C:N}$ denotes the elemental composition of the substrate consumed, calculated as TC/TN (Sinsabaugh et al. 2016).

Bacterial community composition analysis

Soil total genomic DNA was extracted from 1 g of fresh soil samples using MoBio Power Soil DNA extraction kit (MoBio Laboratories Inc. Carlsbad, California, USA) following the manufacturer's instructions and quantified with a Nanodrop UV–vis spectrophotometer (Thermo Fisher Scientific Inc.). The V4-V5 hypervariable regions of the bacterial 16S rRNA gene were amplified using the primer F515/R907 (Walters et al. 2016). PCR amplification was performed using a Gene Amp PCR-System 9700 (Applied Biosystems, Foster City, CA, USA) in a total volume of 20 µl containing 4 µl of 5×FastPfu buffer, 0.4 µl FastPfu DNA polymerase (TransGen Biotech Co. Ltd. Beijing, China), 2 µl of 2.5 mM dNTPs, 0.8 µl of 5 µM of each primer, 10 ng template DNA. The PCR program was as follows: 95 °C for 3 min; 30 cycles of 95 °C for 30 s, 55 °C for 30 s, 72 °C for 30 s, followed by a final extension at 72 °C for 10 min. The triplicate PCR amplicons for each sample were combined and purified through the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA). The product was quantified using Quantus™ Fluorometer (Promega, USA) and pooled for sequencing using 300PE on the Illumina Miseq platform (Illumina, San Diego, CA, USA) at Majorbio Bio-Pharm Technology Co. Ltd. Shanghai, China.

Raw sequence files were preprocessed for optimization by filtering out bad reads using fastp (0.20.0) (Chen et al. 2018) and merging using the Fast Length Adjustment of SHort reads (FLASH) software (V1.2.7, http://ccb.jhu.edu/software/FLASH/) (Magoc and Salzberg 2011). All quality-filtered sequences from 16S rRNA amplicons were clustered into OTUs (Operational Taxonomic Units) at 97% similarity cutoff (Stackebrandt and Goebel 1994) using UPARSE (version 7.1, http://drive5.com/uparse/) (Edgar 2013) followed by chimera filtering. A subset of 29,935 sequences per sample was randomly selected from bacterial 16S rRNA to ensure an equal sampling depth. The raw sequence data have been deposited in NCBI SRA under the BioProject ID of PRJNA816281.

Representative bacterial OTU sequences were taxonomically classified using the Ribosomal Database Project (RDP) classifier (Wang et al. 2007) with a 70% confidence threshold. To simplify the complex response of various bacterial taxa to soil nutrients and environmental variables, we categorized the dominant bacterial taxa into two lifestyles, oligotrophic and copiotrophic, and analyzed changes in the dominance of specific bacterial clades. Likely oligotrophic members include

Acidobacteria, Actinobacteria, and Planctomycetes, while suspected copiotrophic taxa comprise Proteobacteria, Gemmatimonadetes, Firmicutes, and Bacteroidetes (Yang et al. 2022).

Putative function prediction

Bacterial metabolic function associated with nitrogen cycling was predicted by PICRUSt2 based on OTU taxonomical tables (http://huttenhower.sph.harvard.edu/galaxy/) (Douglas et al. 2020). Predicted profiles were annotated based on the Kyoto Encyclopaedia of Genes and Genomes (KEGG) orthology (KO) pathways (Kanehisa et al. 2012). KO terms and metabolic pathways were generated for the OTUs. Changes in the relative abundances of estimates for functional genes were calculated based on the predicted KO abundance.

Statistical analyses

All data were presented as mean ($n=3$) ± standard error (S.E.). Student's t test was conducted to discern differences in plant photosynthetic gas exchange parameters, root traits and biomass, soil physicochemical and biological indicators, as well as the relative abundances of dominant bacterial phyla and potential ecological functions between CT and NT treatments. The natural logarithm transformed response ratio (lnRR) was calculated to further access the effect sizes of tillage treatment on these variables at $P=0.05$ (Luo et al. 2006). The effects are considered significant if the 95% CI of variables do not overlap with zero. The relationships between plant, soil, and microbial community were examined by using Pearson's correlation analysis with the corrplot package in R 4.3.1. Principal Component Analysis analysis (PCA) between plant/soil variables and the relative abundance of dominant bacterial phyla was performed by using Canoco 5.0 software.

Results

Plant physiological traits and soil properties

The aboveground biomass of *C. esculentus* enhanced from 2763.15 kg hm^{-2} under CT condition to 4142.55 kg hm^{-2} ($P<0.05$, Fig. 1) under NT practice. In comparison with CT, NT stimulated photosynthesis of *C. esculentus*, as evidenced by the increased C_i and the declined T_r ($P<0.05$, Fig. 1). NT practice increased the leaf soluble protein content by an average of 76% ($P<0.05$, Fig. 1). The root traits of SRL and SSA increased ($P<0.05$, Fig. 1a), while RD decreased under NT practice ($P<0.05$, Fig. 1a), indicating that NT practice accelerated *C.esculentus* to produce more thinner roots.

NT management increased soil TC and DOC by 19.03% and 86.25%, respectively ($P<0.05$, Fig. 2a), indicating an increment of soil C content, particularly the dissolved organic fraction. Soil NO_3^--N and Olsen P decreased by 39.21% and 35.37%, respectively, under NT treatment ($P<0.05$, Fig. 2b).

NT practice significantly reduced MBN ($P<0.05$, Fig. 3b). The activity of BG was much lower in the NT treatment than in the CT treatment ($P<0.05$, Fig. 3b). NT decreased the BG/NAG ratio by 49.47% ($P<0.05$, Fig. 3a). Soil microbial C limitation index (CLI), as calculated by dividing SIR by BR, tended to increase under NT management ($P<0.05$, Fig. 3b). $S_{C:N}$ and soil microbial CUE were significantly increased by NT practice ($P<0.05$, Fig. 3).

Bacterial community composition and predicted functions

NT significantly reduced soil bacterial α-diversity. The observed OTU numbers (species richness), ACE index, and Shannon diversity decreased by 7.68%, 10.88%, and 1.65%, respectively, under NT treatment ($P<0.05$, Fig. S1). In comparison with CT, NT tended to increase the relative abundance of the so-called oligotrophic bacteria, including Acidobacteria, Actinobacteria, and Planctomycetes; but reduced the relative abundance of the proposed copiotrophic bacterial taxa, such as Proteobacteria, Gemmatimonadetes, Firmicutes, and Bacteroidetes (Fig. 4a, c). The overall oligotroph/copiotroph ratio was significantly higher under NT than under CT treatment ($P<0.05$, Fig. 4b), implying a shift towards an oligotrophs-dominated community.

The potential N metabolism capacity of the bacterial community was predicted by PICRUSt2. Six modules and 35 KEGG orthologs (KOs) for Nitrogen Metabolism (map00910) were extracted from the KEGG orthologue abundance matrix, with 1 module (nitrification) and 13 KOs being significantly impacted by tillage regimes. Obviously, NT practice decreased all the predicted N-cycling processes (Fig. 5a). At the module level, the relative abundance of the M00528 (nitrification) significantly reduced by NT practice ($P<0.05$, Fig. 5a). At the KOs level, nitrification relevant KOs of K10535 (*hao*) and K10946 (*amoC*) decreased by 45.65% and 37.1%, respectively ($P<0.05$, Fig. 5b). Nitrate reduction relevant KOs of K00367 (*narB*) and K15876 (*nrfH*) also decreased under NT practice ($P<0.01$, Fig. 5b). The relative abundances of the KOs involved in the denitrification, including K00368 (*nirK*), K04561 (*norB*), K04747(*norF*), K04748(*norQ*), and K00376 (*nosZ*) were lower in NT than in CT ($P<0.05$, Fig. 5b). The KOs participated in nitrate/nitrite transport ranged from K15576 to K15579, corresponding to the genes of *nrtA* to *nrtD*. NT decreased the relative abundances of the *nrtA–D* genes ($P<0.05$, Fig. 5b). The encoding enzymes, function, and the predicted relative abundances of each KOs were listed in Table S1.

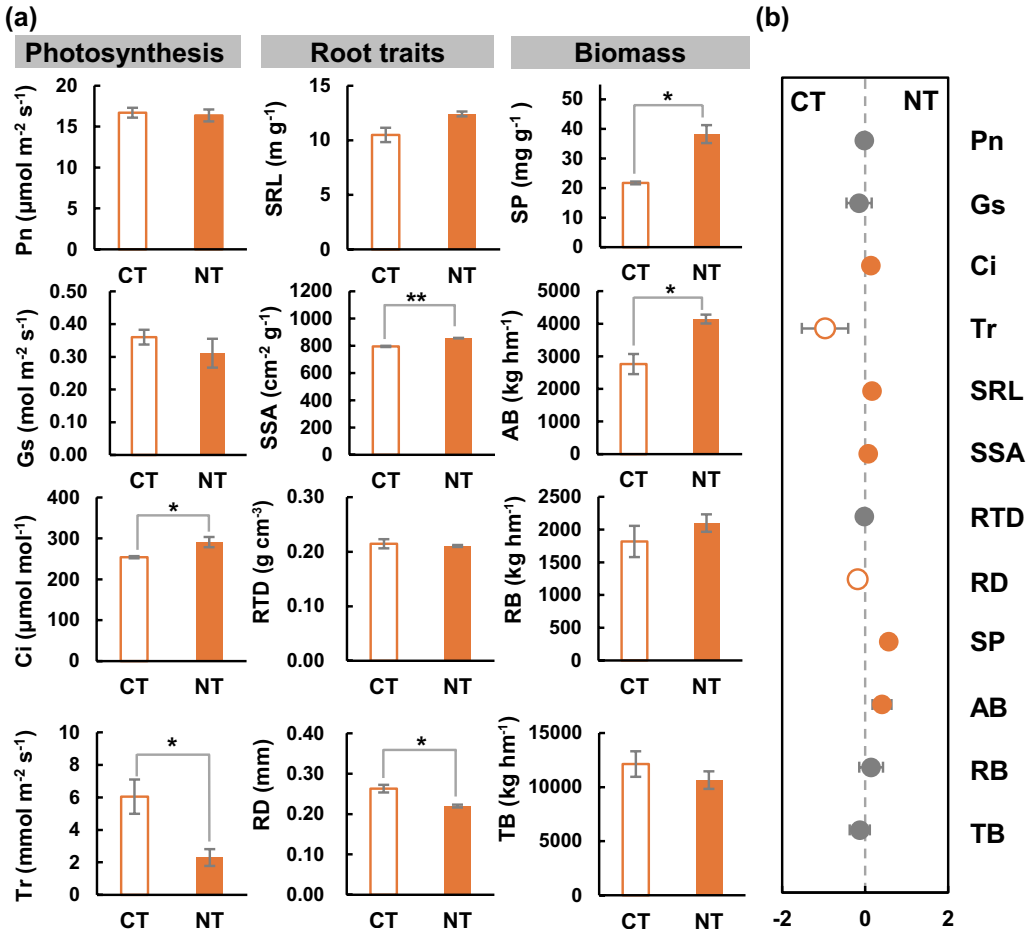


Fig. 1 Impacts of no-tillage on the growth and physiological traits of the *C. esculentus* plant. **a** Comparison of photosynthetic parameters, root traits, soluble protein content, and biomass between CT and NT. Values represent mean ± SE ($n = 3$). Student's *t*-test was performed to determine the tillage management effects (**P* < 0.05, ***P* < 0.01). **b** Effect sizes of NT to CT for plant variables. Values represent mean ± 95% confidence intervals. The dashed vertical line indicates Hedges' *d* (lnRR) = 0. The effects are considered significant if the 95% CIs do not overlap with zero. Orange filled dots indicate a significantly higher effect size under NT. In contrast, orange unfilled dots indicate a significantly higher effect size under CT, and the grey dots represent non-significant effect. *CT* conventional tillage, *NT* no-tillage, *Pn* net photosynthetic rate, *Gs* stomatal conductance, *Ci* intercellular CO_2 concentration, *Tr* transpiration rate, *SRL* specific root length, *SSA* specific root surface area, *RTD* root tissue density, *RD* root diameter, *SP* soluble protein, *AB* aboveground biomass, *RB* root biomass, *TB* tuber biomass

Plant-soil-microbe linkages in *Cyperus esculentus* L. field

Pearson's correlation revealed that soil TC showed positive correlations with plant aboveground biomass, soluble protein content, and C_i. Root biomass, SRL, and SSA were also positively correlated with the TC. Soluble protein content and C_i positively correlated with SRL, SSA, aboveground biomass and root biomass, indicating that the enhanced photosynthesis improved plant aboveground and belowground biomass (Fig. 6a). Soil TC was negatively correlated with soil NO_3^--N and Olsen P. We also observed that soil DOC was positively correlated with soluble protein content, photosynthesis (C_i), aboveground biomass, and root growth (root biomass, SRL, and SSA). Soil TC was positively correlated with soil microbial C limitation index (CLI) and CUE. Soil oligotrophs/copiotrophs ratio tended to be positively correlated with soil TC, as well as microbial CLI and CUE; but was negatively correlated with NO_3^--N and Olsen P (Fig. 6a).

The PCA analysis was fairly consistent with the Pearson's correlation. It was observed that the NT plots were loaded on the negative direction of *X*-axis, associating with soil TC, NH_4^+-N, DOC, plant growth (aboveground biomass, root biomass, SRL, SSA, soluble protein content), photosynthesis (C_i), microbial C demand (CLI), carbon use efficiency (CUE), and the nominated oligotrophic taxa, including Acidobacteria, Actinobacteria, and Planctomycetes (Fig. 6b). It indicated that these

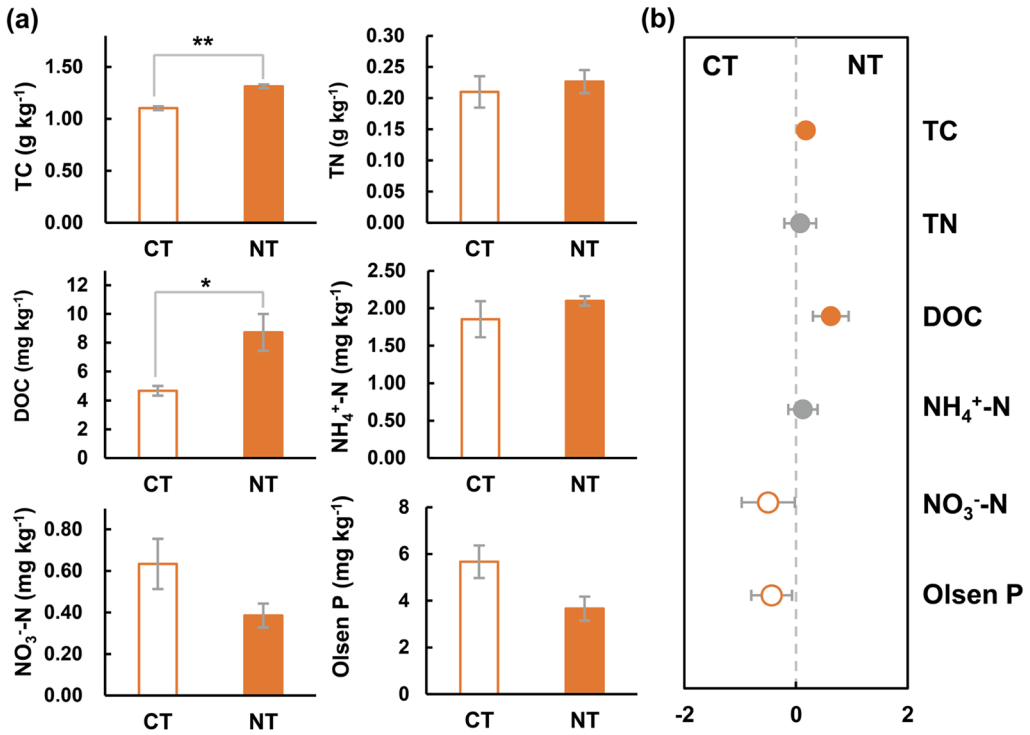


Fig. 2 Impacts of no-tillage on soil chemical properties. **a** Comparison of soil carbon and nutrients content between CT and NT. Values represent mean ± SE ($n = 3$). Student's *t*-test was calculated to determine the tillage management effects (*$P < 0.05$, **$P < 0.01$). **b** Effect sizes of NT to CT for each variable. Values represent mean ± 95% confidence intervals. The dashed vertical line indicates Hedges' *d* (lnRR) = 0. The effects are considered significant if the 95% CIs do not overlap with zero. Orange filled dots indicate a significantly higher effect size under NT. In contrast, orange unfilled dots indicate a significantly higher effect size under CT, and the grey dots represent non-significant effect. *CT* conventional tillage, *NT* no-tillage, *TC* total carbon, *TN* total nitrogen, *DOC* dissolved organic carbon

plant-soil-microorganism parameters were synergistically enhanced by NT practice, and there are positive correlations among these variables. In contrast, CT samples were loaded on the positive direction of *X*-axis, along with soil available N and P nutrients, plant growth (tuber biomass, RD), T_r, qCO_2, and the relative abundance of the so-called "copiotrophic" bacterial phyla of Proteobacteria, Gemmatimonadetes, Firmicutes, and Bacteroidetes, implying negative impacts of NT on these parameters. It also suggested that the relative abundance of the copiotrophic bacterial taxa were positively correlated with soil NO_3^--N and Olsen P (Fig. 6b).

Discussion

In this research we aimed to: (i) investigate the effects of NT practice on soil TC content in a sandy agroecosystem and (ii) elucidate the mechanisms underlying these effects. Our findings revealed that NT increased soil TC content, indicating its potential to enhance C storage in this sandy agroecosystem. We proposed that NT might contribute to soil TC content through increasing plant-derived C inputs, enhancing soil microbial CUE, and shifting the soil microbial community towards a dominance of oligotrophic taxa (Fig. 7).

No-tillage practice increased soil TC content by increasing plant-derived carbon

In consistent with a variety of previous studies (Wright et al. 2007; Hurisso et al. 2013; Wang et al. 2019), we observed that NT management increased soil TC content in sandy soils in Horqin sandy land, even within one-year of experiment. The rapid response of soil TC content to NT might rely on the low initial TC content level and the poor aggregation in sandy soils (Chagas et al. 2022). The enhancement of soil TC content under NT conditions might attribute to complex mechanisms. Previous researches recommended that NT is beneficial for the accumulation of SOC by increasing plant-derived C (Gale and Cambardella 2000; Crow et al. 2018; Vezzani et al. 2018; Gao et al. 2021; Tian et al. 2024). It was proposed that NT could increase crop photosynthesis, soluble protein and biomass through improving surface soil nutrients and water content (Elyasi et al. 2023), which subsequently increase the belowground deposition of photo-assimilated C, including root residues and

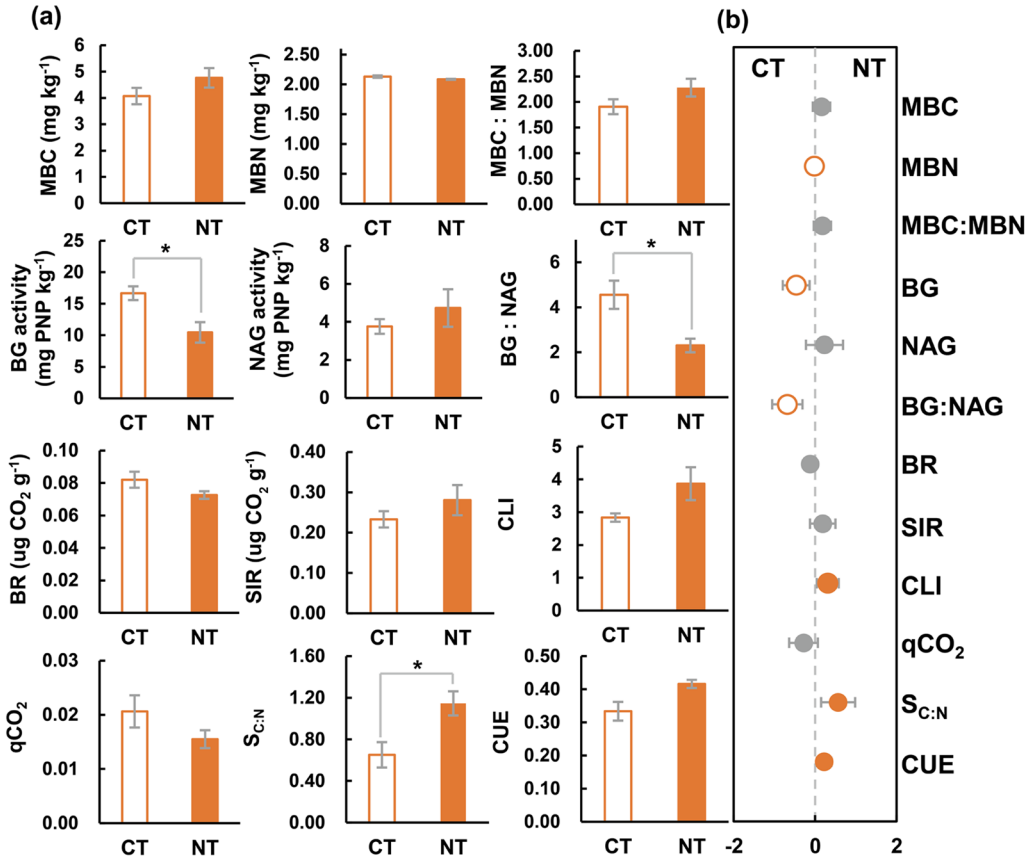


Fig. 3 Impacts of no-tillage on soil microbial properties. **a** Comparison of soil microbial biomass, soil enzyme activities, soil respiration, carbon limitation index, metabolic quotient and carbon use efficiency between CT and NT. Values represent mean ± SE ($n = 3$). Student's *t*-test was calculated to determine the tillage management effects (*$P < 0.05$). **b** Effect size of NT to CT for each variable. Values represent mean ± 95% confidence intervals. The dashed vertical line indicates Hedges' *d* (lnRR) = 0. The effects are considered significant if the 95% CIs do not overlap with zero. Orange filled dots indicate a significantly higher effect size under NT. In contrast, orange unfilled dots indicate a significantly higher effect size under CT, and the grey dots represent non-significant effect. *CT* conventional tillage, *NT* no-tillage, *MBC* microbial biomass carbon, *MBN* microbial biomass nitrogen, *BG* β-1,4-glucosidase, *NAG* N-acetyl-β-D-glucosaminidase, *BR* basal respiration, *SIR* substrate-induced respiration, *CLI* soil microbial C limitation index, qCO_2 metabolic quotient, *CUE* carbon use efficiency

exudates (Govaerts et al. 2009; Zhu et al. 2019; Crow et al. 2020; Rodrigues et al. 2022). The findings in this sandy arable fields generally supported these propositions. We observed that NT practice increased aboveground biomass and photosynthesis (C_i, Fig. 1a), and there is a positive correlation among aboveground biomass, C_i and soil TC content. In addition, NT management tended to increase SSA and SRL, and thus, might increase the root residues and root exudates (Fig. 1b). Root residues and rhizodeposits are important source for SOC accumulation, in particular in the forms of dissolved organic compounds (Dou et al. 2008; Mo et al. 2019). It implies that the increase in TC content is mainly attributed to the sharp increase in soil DOC under NT management (Fig. 2a). The allocated DOC can be further stabilized and transferred into stable soil C through the sorption of C to reactive mineral surfaces and ultimately building soil C stocks (Liebmann et al. 2020). Our findings suggested that, in the highly sandy agricultural ecosystem, NT practice can have a distinct advantage in soil C sequestration by enhancing plant photosynthesis, aboveground-belowground biomass and thus the plant-derived DOC.

No-tillage practice increased soil TC content through increasing soil microbial CUE

In this study, we observed that NT practice increased microbial CUE (Fig. 3) and soil TC (Fig. 6a), implying that NT might enhance soil C storage by improving soil microbial CUE. A variety of previous studies consistently documented that NT practice is beneficial for improving soil microbial CUE (Sauvadet et al. 2018; Song et al. 2022; Zhang et al. 2022; Tian et al. 2024), nonetheless, the underlying mechanisms are not explicitly explained. In this research, we proposed that the enhanced microbial

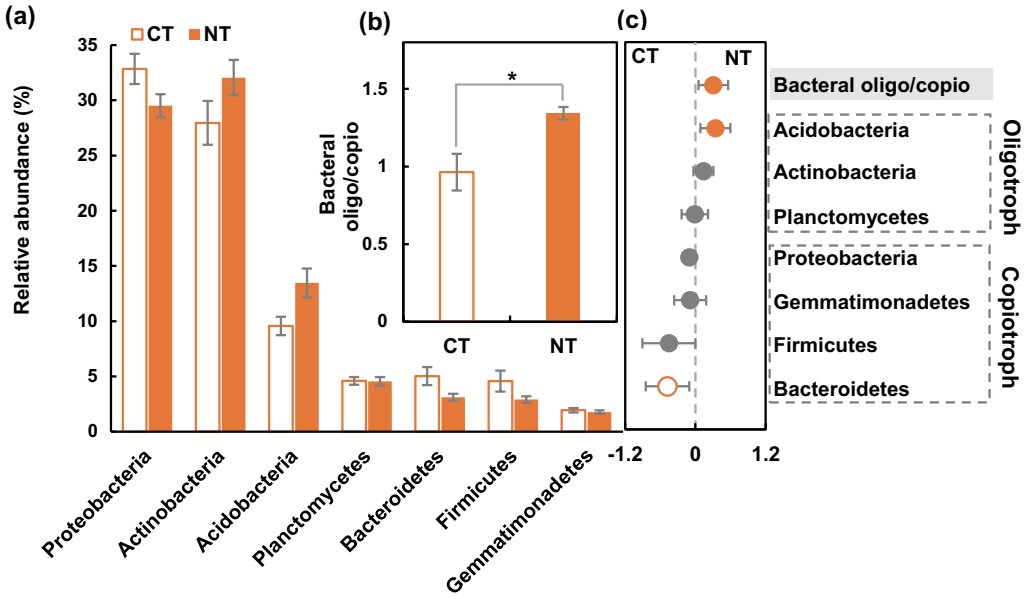


Fig. 4 Impacts of no-tillage on the relative abundance of dominant bacterial phyla. **a** Comparison of the relative abundances of dominant bacterial phyla between CT and NT. **b** The oligotrophs/copiotrophs ratio of bacterial community. Values represent mean ± SE ($n = 3$). Student's *t*-test was used to determine the tillage management effects (*****$P < 0.05$). **c** Effect sizes of NT to CT for each bacterial phylum. Values represent mean ± 95% confidence intervals. The dashed vertical line indicates Hedges' *d* (lnRR) = 0. The effects are considered significant if the 95% CIs do not overlap with zero. Orange filled dots indicate a significantly higher effect size under NT. In contrast, orange unfilled dots indicate a significantly higher effect size under CT, and the grey dots represent non-significant effect. *CT* conventional tillage, *NT* no-tillage

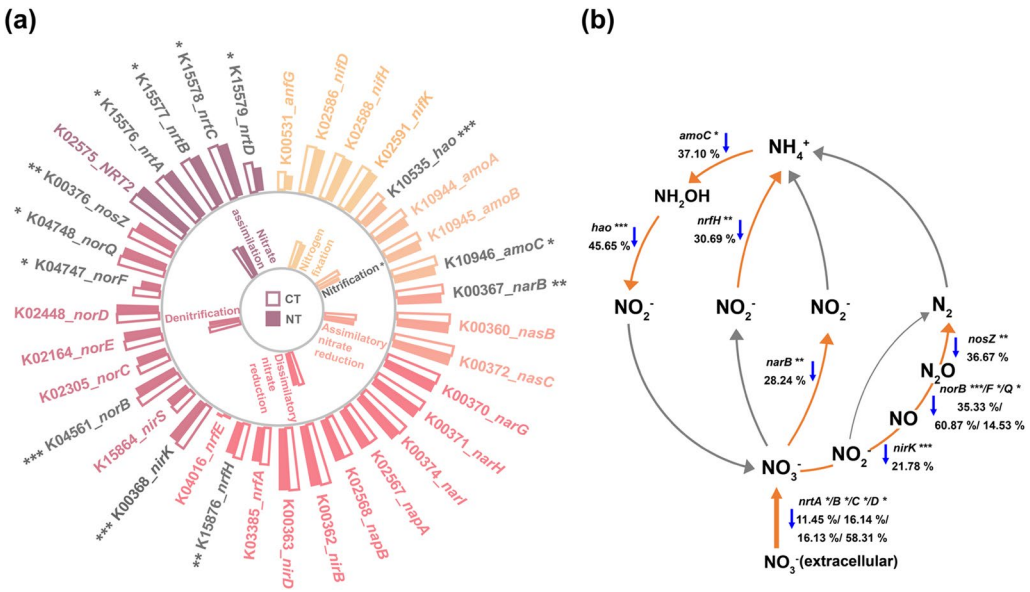


Fig. 5 Putative bacterial functions affiliated with N cycling predicted by PICRUSt2. **a** A circular barplot showing the abundance of KOs and modules from KEGG map00910 (Nitrogen metabolism). The abundance of KOs and modules were log-transformed. The response ratio (lnRR) was calculated to determine the tillage management effects (*****$P < 0.05$, ******$P < 0.01$, *******$P < 0.001$). **b** Changes of the predicted genes involved in the N cycling. Only the significant statistical results ($P < 0.05$) were labeled on the figure. The percentage labeled next to the functional gene indicating the relative change in NT compared to CT. The straight blue arrows indicate the decrease in NT compared to CT. The curved orange and grey arrows indicate significant and non-significant relationships, respectively. *CT* conventional tillage, *NT* no-tillage

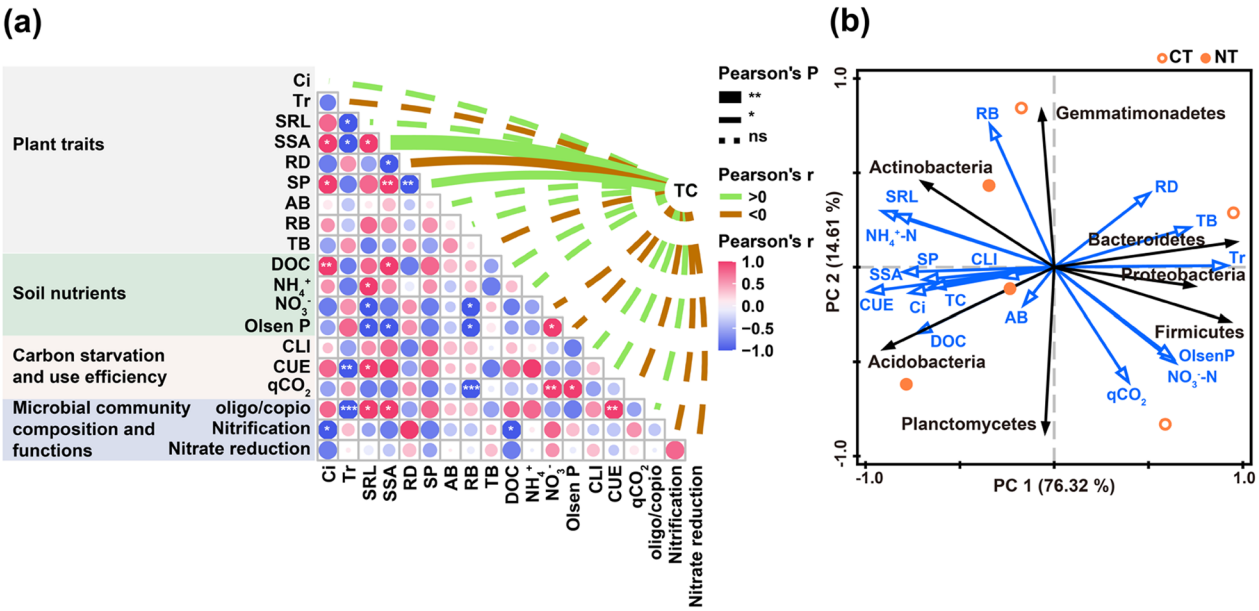


Fig. 6 Plant-soil-microbe linkages in *Cyperus esculentus* L. field. **a** Pearson's correlation analysis between TC and plant traits, soil nutrients, carbon availability and use efficiency, and microbial community composition and functions. The correlation coefficients ranging from negative to positive are indicated by color intensity changing from blue to pink, as illustrated by the figure legend. The significant statistical results were labeled in the figure (*****$P < 0.05$, ******$P < 0.01$, *******$P < 0.001$). Edge colors indicate positive and negative correlations and line shapes indicate statistical significance. **b** principal component analysis (PCA) of dominant bacterial phyla under different tillage management. The loadings for the phyla were shown by the black vectors. Plant traits, soil nutrients, carbon availability, and use efficiency were used as the environmental factors represented by blue arrows. *CT* conventional tillage, *NT* no-tillage, *TC* total carbon, *Ci* intercellular CO_2 concentration, *Tr* transpiration rate, *SRL* specific root length, *SSA* specific root surface area, *RD* root diameter, *SP* soluble protein, *AB* aboveground biomass, *RB* root biomass, *TB* tuber biomass, *DOC* dissolved organic matter, *CLI* soil microbial C limitation index, qCO_2 metabolic quotient, *CUE* carbon use efficiency, *oligo/copio* bacterial oligotroph/copiotroph ratio

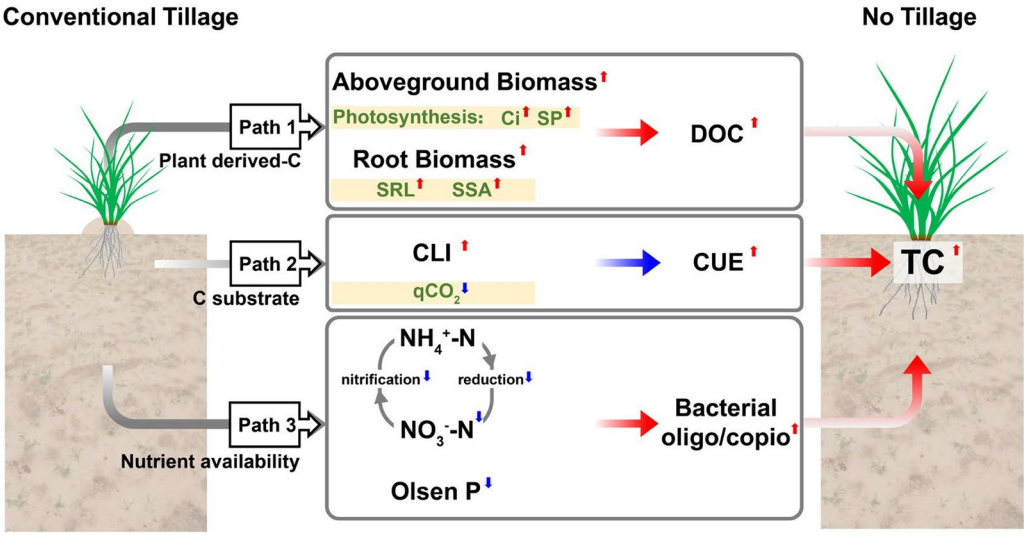


Fig. 7 Conceptual diagram illustrating the potential mechanisms for improving the soil TC content of sandy soil under NT practice. NT practice increased soil TC content through three pathways. (i) Enhancing soil DOC content by increasing the aboveground-belowground biomass, photosynthesis, and thus, the plant-derived dissolved organic C (DOC); (ii) increasing CLI and thus increasing soil microbial CUE; (iii) increasing the prevalence of oligotrophic members in bacterial communities by decreasing available nitrogen and phosphorus nutrient levels. The red arrows indicate the positive effects of NT practice, whereas the blue arrows indicate the negative effects. *Ci* intercellular CO_2 concentration, *SP* soluble protein content, *SRL* specific root length, *SSA* specific root surface area, *DOC* dissolved organic carbon, *CLI* soil microbial C limitation index, qCO_2 metabolic quotient, *CUE* carbon use efficiency, *TC* total carbon

CUE under NT practice might be due to the increased microbial demands for C. We determined the soil microbial C limitation index (CLI) by dividing substrate-induced respiration (SIR) by basal respiration (BR) (Hou et al. 2019). When available C resources are scarce, soil microbes are "C starvation". As a consequence, soil microorganisms responded strongly to glucose addition, resulting in a high SIR and a high microbial CLI value. Thus, a high CLI value implies a C deficit for microbial community and a high C demand, whereas a low microbial C starvation index value represents a C-saturated status. In this study, it was observed that NT practice increased soil microbial CLI, and positively correlated TC with CLI (Figs. 3b and 6a).

A declined microbial metabolic quotient (qCO_2) was observed under NT conditions, along with an increase in CUE. Compared to CT, NT management typically increased soil bulk density and water-filled porosity, which impeded oxygen diffusion through the soil profile. Since soil microbes require oxygen for aerobic respiration, NT management ultimately reduced the carbon loss as CO_2 from microbial respiration. In combination with higher MBC/MBN under NT practice (Fig. 3a), it implies that relatively less C was partitioned into heterotrophic respiratory of CO_2-C in comparison with the biomass C stored by microbial assimilation (Xu et al. 2017; Ren et al. 2021). These findings further supported the increased CUE under NT practice, which is helpful for soil C sequestration.

No-tillage practice increased soil TC content by increasing the prevalence of oligotrophic members

Though the impacts of NT practice on soil microbial community composition are not extensively explored, most of the exist publications revealed that NT induced compositional shifts in microbial copiotrophic/oligotrophic cascade (Kim et al. 2020; Degrune et al. 2017; Yin et al. 2017). It was generally documented that taxa featuring more copiotrophic lifestyles, such as Bacteroidetes (Yin et al. 2017; Pratibha et al. 2023), Firmicutes (Pathan et al. 2021), Gemmatimonadetes (Carbonetto et al. 2014), and Protebactria (Degrune et al. 2017) were more abundant under CT practice, whereas NT practice favoring the dominance of oligotrophic bacterial taxa with the increased abundance of Acidobacteria (Kim et al. 2020), Actinobacteria (Zhang et al. 2024), and Planctomycetes (Pathan et al. 2021). In consistent with previous findings, the present study found that NT practice decreased the relative abundances of copiotrophic taxa and increased oligotrophs/copiotrophs ratio in the selected sandy arable fields (Fig. 4). Still, there is a positive correlation between oligotrophs/copiotrophs ratio and TC (Fig. 6a), suggesting that NT practice might improve soil TC content through shifting soil bacterial community towards an oligotrophic cascade. The shifts towards an oligotrophs-dominant community might depend on the increased C resource limitation status and the declined availability of nitrogen and phosphorus nutrients under NT management (Figs. 2b and 3b).

The impacts of NT on soil available N are highly debated. Soil NO_3^--N contents might increase (Zulu et al. 2023), decrease (García-Gutiérrez et al. 2023) or remain unchanged (Waring et al. 2024) under NT conditions, in comparison with CT. In sandy dry farmlands, NT practice typically decreased NO_3^--N content, as observed in this and a previous research conducted in the semiarid region in eastern Montana, USA (Sainju et al. 2009). It was proposed that tillage can cause a greater N mineralization due to soil disturbance, and thus, NO_3^--N was greater in CT than NT (Malhi et al. 2001; Patra et al. 2004). In this research, we found that the NT practice had notable negative effects on predicted nitrate reduction, nitrification, and denitrification processes (Fig. 5a, b), corresponding exactly to the sharp decreases in NO_3^--N. The texture of the aeolian sandy soil, which consists of fine sand with poor water and fertilizer retention, would also lead to the low nutrient content. The declined N stimulated the activity of N acquiring enzyme (NAG) compared with C acquiring enzyme (BG), leading to a decrease in BG/NAG. We still observed a decrease in Olsen P under NT practice, further causing an oligotrophic habitat and shifting soil bacterial community towards the dominance of oligotrophic taxa (Wang et al. 2020). Since the prevalence of oligotrophic taxa is recommended to be associated with recalcitrant C pool and beneficial for C stabilization (Li et al. 2021), shifts towards an oligotrops-dominant community might be an important mechanism for driving the improvement of C storage under NT practice.

Conclusions

In this research, we investigated the response of TC content under NT and CT practices in a sandy *C. esculentus* field, and explored the underlying mechanisms. We concluded that NT practice could improve soil total C content within a one-year experiment in this sandy arable field, which may rely on three possible aspects. First, NT management increased the plant-derived C by increasing the photosynthesis and biomass. The improved plant-derived C promotes soil DOC and the TC content. Second, NT increased soil microbial CUE and decreased metabolic quotient (qCO_2), which ultimately increased the C immobilized in microbial biomass. Third, NT increased the prevalence of oligotrophic members in bacterial communities by

decreasing available nitrogen and phosphorus levels, which is beneficial for alleviating the loss of soil C. The current study enriched our knowledge on the impacts of NT practice on soil TC content and the underlying mechanism in sandy arable lands. The generated findings are helpful for modifying tillage practice to meet the requirements of both increasing crop yields and alleviating C loss in sandy lands.

Abbreviations

AB	Aboveground biomass
BR	Basal respiration
C	Carbon
C_i	Intercellular CO_2 concentration
CLI	Soil microbial C limitation index
CT	Conventional tillage
CUE	C use efficiency
DOC	Dissolved organic carbon
G-	Gram-negative
G+	Gram-positive
G_s	Stomatal conductance
KEGG	Kyoto Encyclopaedia of Genes and Genomes
KO	KEGG orthology
lnRR	Natural logarithm transformed response ratio
MBC	Microbial biomass C
MBN	Microbial biomass N
NH_4^+-N	Ammonium nitrogen
NO_3^--N	Nitrate nitrogen
NT	No-tillage
Olsen P	Plant readily available phosphorus
PAR	Photosynthetically active radiation
PCA	Principal Component Analysis analysis
PLFA	Phospholipid fatty acid
P_n	Net photosynthetic rate
qCO_2	Metabolic quotient
RB	Root biomass
RD	Root diameter
RDP	Ribosomal Database Project
RTD	Root tissue density
SIR	Substrate-induced respiration
SOC	Soil organic carbon
SOM	Soil organic matter
SP	Soluble protein
SRL	Specific root length
SSA	Specific root surface area
TB	Tuber biomass
TC	Total carbon
TN	Total nitrogen
TOC	Total organic carbon
T_r	Transpiration rate

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-024-00573-x.

Supplementary material 1: Fig. S1 The α-diversity of the microbial community between CT and NT. Values represent mean ± SE ($n = 3$). Student's t-test was calculated to determine the tillage management effects. (*$P < 0.05$, **$P < 0.01$) *CT* conventional tillage, *NT* no-tillage. Table S1 Functional annotation and relative abundance of genes in nitrogen metabolism pathway (KO00910) under different tillage management

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Author contributions

Cong Wang: data curation, visualization, writing—original draft. Yuxiang Hu: formal analysis, investigation, methodology. Hui Wu: formal analysis, investigation. Zhirui Wang: formal analysis, investigation. Jiangping Cai: funding acquisition. Heyong Liu: project administration. Wei Ren: resources. Ning Yang: resources. Zhengwen Wang: resources. Yong Jiang: funding acquisition, resources. Hui Li: conceptualization, funding acquisition, supervision, writing—review & editing.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors agreed and approved the manuscript for publication in Ecological Processes.

Competing interests

The authors declare that they have no competing interests.

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