Received: 31 March 2021 | Revised: 18 June 2021 | Accepted: 3 July 2021

DOI: 10.1111/ejss.13143

ORIGINAL ARTICLE

European Journal of Soil Science WILEY

Long-term irrigation reduces soil carbon sequestration by affecting soil microbial communities in agricultural ecosystems of northern China

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Funding information
The Strategic Priority Research Program of Chinese Academy of Sciences, Grant/Award Number: XDB40020203; National Natural Science Foundation of China, Grant/Award Numbers: 41771278, 41930865, 41001060; US National Science Foundation; European Research Council, Grant/Award Number: ERC-SyG-2013-610028 IMBALANCE-P

Abstract

Irrigation has become one of the main approaches to improve agricultural production in an arid area. The variation of soil moisture after irrigation has the potential to affect soil microbial community composition and soil organic carbon (SOC) storage, and thus, the imbalances in the terrestrial ecosystem carbon cycle. However, the impact of long-term irrigation on the relationships between soil microbial community and SOC sequestration in semiarid agroecosystems is still poorly understood. We took advantage of a 7-year irrigation experiment in a winter wheat-maize rotation system in northern China, whereby the non-irrigation was subject to rain-fed conditions. We aimed to investigate the effects of long-term irrigation on soil microbial communities and their linkages with soil carbon sequestration. Seven years of irrigation significantly increased soil moisture content by 39% but decreased SOC concentration of topsoil (0–20 cm) by 4.2% on average across all sampling times. The responses of soil microbial communities to irrigation were highly taxa dependent. Irrigation significantly decreased fungal biomass, fungal-to-bacterial ratio and Gram-positive-to-Gram-negative bacterial ratio, and did not affect the bacterial community biomass. The decreased SOC concentration under the long-term irrigation was mainly caused by the changes in the ratio of fungi-to-

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bacteria. Our findings highlight the important role of soil fungal-to-bacterial ratio in mediating the response of SOC dynamics to a future drier climate in semiarid agricultural ecosystems.

Highlights

Irrigation influences the soil microbial community and carbon stock in semi-arid agroecosystems.

Highlights the role of fungi:bacteria ratio in mediating the response of SOC dynamics to irrigation

Long-term irrigation decreased soil carbon content by changing the microbial community.

Reduced SOC storage after irrigation was due to the decreased ratio between fungi and bacteria.

KEYWORDS

fungi, Gram-negative bacteria, Gram-positive bacteria, semiarid agricultural systems, soil carbon, soil microbial community composition, soil moisture

1 | INTRODUCTION

Long-term sustained severe drought can strongly decrease crop production, and thus affect food supply and food security (Lesk, Rowhani, & Ramankutty, 2016). The North China Plain is the main grain-producing area, with frequent occurrence of the severe drought seen in China (Zhang, Chen, & Zhang, 2019). Therefore, intensive irrigation has become the main practice to increase crop yield in this region. Irrigation not only influences soil physical processes (such as water infiltration and leaching) but also affects biotic processes (such as crop growth) in agroecological ecosystems (Du et al., 2018). However, previous studies mainly focused on the effect of soil moisture variation after irrigation on aboveground carbon (C) processes, such as leaf photosynthesis and aboveground net primary productivity (Jafarikouhini, Kazemeini, & Sinclair, 2020; Wang, Hu, Liu, Ahmad, & Zhou, 2021). In contrast, the responses of belowground carbon processes to long-term irrigation are unclear, especially the effect of the soil microbial community in this process.

The variation of soil moisture after irrigation will affect soil microbial community composition through its effect on microbial physiological tolerance and metabolic capacity (Kaisermann et al., 2013). As a consequence, the adaptive microbial strategy will shift, resulting in changes in the composition and functioning of soil microbial communities (Evans, Wallenstein, & Fierer, 2014). Therefore, the variation of soil moisture may not only influence the physical characteristics of the soil and soil nutrient diffusion to microorganisms but also act as an environmental filter shaping the physiological response and composition of soil microbial communities.

Some bacterial strains adjust their osmotic pressure mechanisms in response to rapid changes in soil water potential (Sleator & Hill, 2002). Bacterial communities exhibit a highly conservative recovery strategy dependent on phylogeny and can rapidly synthesize proteins in response to wetting events or seasonal rainfall patterns (Ruehr et al., 2009). For instance, Gram-positive bacteria generally grow more slowly than Gram-negative bacteria and are considered *K*-strategists, because they show slower development, larger body size, delayed reproduction and longer lifespan (Punsalang, Healmbbs, & Murphy, 1989). A high abundance of Gram-positive bacteria under lower moisture is associated with their thicker cell wall and greater drought tolerance (Chodak, Golebiewski, Morawska-Ploskonka, Kuduk, & Niklinska, 2015; Hueso, Garcia, & Hernandez, 2012), whereas Gram-negative bacteria are more sensitive to major changes in water potential (Nesci, Etcheverry, & Magan, 2004). In addition, the ability of many Gram-positive bacteria to sporulate allows them to recover quickly after disturbance (Drenovsky, Steenwerth, Jackson, & Scow, 2010). Therefore, the resistance of the microbial community to disturbance may increase the ratio of Gram-positive and Gram-negative bacterial biomass or the relative abundance of Gram-positive bacteria.

Another important group among soil microorganisms, soil fungi, are considered more tolerant to the variation of soil moisture than bacteria because extensive fungal hyphal networks allow them to internally transfer moisture and nutrients in a disturbed environment.

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Fungi generally have a lower nutrient requirement than bacteria (de Boer, Folman, Summerbell, & Lynne, 2005; Rousk et al., 2010; Strickland & Rousk, 2010). Further, fungal chitinous cell walls make them more resistant and resilient than bacteria to variations in water availability (Guggenberger, Frey, Six, Paustian, & Elliott, 1999). In addition, mycorrhizal fungi can obtain assimilation products from plants and in return promote water and nutrient supply because they are directly connected to roots (de Deyn, Quirk, Oakley, Ostle, & Bardgett, 2011; Jones, Nguyen, & Finlay, 2009). Hence, the abundance of fungi tends to be greater than that of bacteria in lower soil moisture, and the fungi-to-bacteria ratio increases when a greater resistance of microbial communities against drought stress is required (Preece, Verbruggen, Liu, Weedon, & Peñuelas, 2019). However, the effects of soil moisture on the microbial community composition are inconsistent, and some studies found a relatively higher ratio of fungi and Gram-positive bacteria in conditions of low soil moisture (Barnard, Osborne, & Firestone, 2013; Fuchslueger, Bahn, Fritz, Hasibeder, & Richter, 2014; Preece et al., 2019), whereas others showed limited or almost no influence on the microbial community composition (Canarini, Carrillo, Mariotte, Ingram, & Dijkstra, 2016; McHugh & Schwartz, 2015; Rousk, Smith, & Jones, 2013).

In terrestrial ecosystems, soil microorganisms play an important role in the soil carbon cycle because they can mineralize SOM, and they convert soil carbon into CO_2 then release it into the atmosphere (Bardgett, Freeman, & Ostle, 2008; Bruun, Clauson-Kaas, Bobulska, & Thomsen, 2014). The relative contributions of fungal and bacterial functional groups to SOM decomposition differ (Wang et al., 2014). In some cases, the carbon assimilation efficiency of bacteria is lower than that of fungi, and the fungal storage carbon is much greater than bacterial storage carbon (Suberkropp & Weyers, 1996). In addition, fungal-dominated soil microbial communities can improve soil carbon stability and generate more stable carbon (Bardgett et al., 2008; Zhang et al., 2019). Therefore, soil moisture can influence the soil carbon cycle through changes in soil microbial community composition (Borken & Matzner, 2009; Lei et al., 2016; Su et al., 2020).

In this study, we took advantage of a 7-year irrigation experiment in a winter wheat-maize rotation system in northern China. The annual precipitation during the experimental period varied from 330 to 576 mm. A high crop yield in this region is mainly achieved by intensive irrigation (Xiao et al., 2016). The field treatments included irrigation plots and non-irrigation plots (only rain-fed conditions). We aimed to investigate how long-term irrigation affects the soil microbial community composition and the soil carbon stock in a semiarid agroecosystem. We hypothesized that: (a) long-term irrigation would decrease the ratio of fungi and bacteria, as well as the ratio of Gram-negative and Gram-positive bacteria; and (b) the variation of soil microbial community composition under long-term irrigation would decrease the soil carbon stock. The findings of this study will advance our understanding of the relationship between microbial community composition and soil carbon cycling in future precipitation regimes.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

This study was conducted at the Luancheng Agroecosystem Experimental Station (37°53′N, 114°41′E, 50.1 m a.s.l.), located in the high-yield zone of the North China Plain. The climate of this study area is a semiarid warm temperate continental monsoon with a mean annual temperature of 12.3°C. About 75% of the annual precipitation occurs in the summer (June–September). The soils are classified as silt loam Haplic Cambisol according to the Food and Agriculture Organization (FAO) soil taxonomy system. The basic information on topsoil (0–20 cm) was listed as follows: soil organic matter (SOM), 12–13 g kg^{-1}; total nitrogen (N), 0.7–0.8 g kg^{-1}; soil available N, 60–80 mg kg^{-1}; soil available phsophorus (P), 15–20 mg kg^{-1}; soil available potassium (K), 150–170 mg kg^{-1}; saturated volumetric water content, 44.1%; water holding capacity, 35.4%. The cropping system in this area is winter wheat-maize rotation with winter wheat grown from early October to mid-June and maize grown following wheat harvest.

Field irrigation experiments were set up at the research station in 2006 and have been maintained since then. A completely randomized block design was used, with four plots (5 m in width, 10 m in length and 1.5 m in depth) assigned to an irrigation treatment and three plots assigned to a non-irrigation (rainfed) treatment. The irrigated plots received sufficient water to maintain the soil moisture content of the 1-m soil profile near field capacity (~75% of water-holding capacity). Irrigation timing was mainly determined according to the key growth period of crops and was consistent with local farmers' irrigation practices. The non-irrigated plots were subject to the rainfed condition, and only received natural precipitation without extra irrigation during the experimental period. Due to an unfortunate event, one of the non-irrigated plots was destroyed, so there were only three replicates of the non-irrigated treatment. To avoid

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the effects of plants and soil outside the plots, the plots were separated by concrete walls (1,500 mm deep, 200 mm tall and 245 mm thick) according to FAO standards. Based on local historical planting and fertilization regimes, the winter wheat cultivar Kenong 199 was sown in early October at a seed rate of 150 kg ha^{-1} with a 20-cm row space and harvested in mid-June in the following year: 600 kg ha^{-1} of nitrogen and phosphorus compound fertilizer ($(NH_4)_2HPO_4$) and 150 kg ha^{-1} of urea fertilizer ($CO(NH_2)_2$) were applied before wheat sowing; 300 kg ha^{-1} of urea fertilizer was applied at the jointing stage of winter wheat. The maize cultivar Zhengdan 958 was sown at a density of 60,000 plants ha^{-1} in mid-June and harvested in early October: 500 kg ha^{-1} of urea fertilizer was applied in late July during the maize growing season. All field management practices were uniformly applied to the irrigation treatment plots and non-irrigation plots.

2.2 | Sample collection and analysis

The inner 3 m × 8 m area of each plot was used for sampling plant and soil, with the outer 2 m serving as a buffer zone. Soil volumetric moisture content in a 1.8-m soil profile was measured using a neutron probe (aboveground 20 cm and belowground 180 cm; Institute of Hydrology, Wallingford, UK) at 200-mm intervals in the centre of the plot every 7–15 days. Daily air temperature and precipitation were monitored automatically by the weather station at the research station. The choice of sampling time is based on the different plant growth periods and included different seasons. The soil sampling time was usually before irrigation or at a sufficiently long time after the last irrigation in order to exclude short-term effects of specific irrigation events on soil microorganisms. Topsoil (0–200 mm) was sampled from each plot by using a soil corer (38 mm in diameter). Soil sampling in 2013 focused on the wheat-growing season, including the wheat-jointing stage (4 April), grain-filling stage (15 May), seedling emergence stage (12 October) and initial winter stage (22 November). Soil sampling in 2014 focused on maize growth periods, including wheat jointing (9 April), maize seedling emergence (12 June) and maize jointing (8 July). In each plot, at least five soil samples were taken randomly, homogenized, and bulked into one composite sample. Each composite sample was split in two after the surface organic material and visible roots were carefully removed. One-half of the sample was air-dried for analysis of soil physicochemical properties and the other was stored at −20°C for microbial analysis after sieving to 2 mm.

Soil moisture content in the samples was determined gravimetrically after drying for 24 h at 105°C. Soil pH was determined in a 1:2.5 ratio of soil and water slurry using a combination glass electrode. Soil organic carbon (SOC) was determined with the $K_2Cr_2O_7$ titration method after digestion (Lu, 1999). Available N was determined with an alkaline hydrolysis diffusion method (Lu, 1999). Available P was extracted with 0.5 M $NaHCO_3$ solution (pH = 8.5) and determined by the Mo-Sb colorimetric method (Lu, 1999). Soil microbial community composition was characterized using phospholipid fatty acid (PLFA) analysis, as described by Frostegård and Bååth (1996) with minor modifications. Briefly, 8 g freeze-dried soil samples were extracted in a chloroform-methanol-phosphate buffer (1:2:0.8 v/v/v), and the extracted lipids were fractionated into neutral lipids, glycolipids and polar lipids on silica acid columns by successive elution with chloroform, acetone and methanol, respectively. The methanol fraction (containing phospholipids) was subjected to mild alkaline methanolysis to transform the fatty acids into free methyl esters and analysed on a gas chromatograph (Agilent Technologies 7890B, USA) equipped with a flame ionization detector. Peaks were identified using bacterial fatty acid standards and MIDI peak identification software (MIDI, Inc., Newark, DE, USA). The PLFAs *i*15:0, *a*15:0, *i*16:0, *i*17:0 and *a*17:0 were used to indicate Gram-positive (GP) bacteria, and the PLFAs 16:1ω9c, 16:1ω7c, 18:1ω7c, cy17:0 and cy19:0 were used to indicate Gram-negative (GN) bacteria (Frostegård & Bååth, 1996; Zelles, 1999). The sum of PLFA markers chosen to represent Gram-positive and Gram-negative bacteria was used to determine total bacteria. The PLFA 18:2ω6c was used as an indicator of fungi. The PLFAs were chosen to represent fungi and the sum of the PLFA markers chosen to represent bacteria was used to calculate the fungi-to-bacteria ratio. All PLFAs were expressed as nmol g^{-1} dry soil.

2.3 | Statistical analysis

All data were checked for normal distribution and homogeneity of variance before statistical analysis and all values were presented as means ± standard error (*SE*). The effects of treatment, sampling time and their interactions on soil properties and microbial indices were tested using two-way repeated-measures ANOVA. Multivariate dimensionality reduction analysis was applied to quantify and test the effects of treatment and environmental factors on the variation of soil microbial community composition. All the above analyses were performed in SPSS

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Statistics 20.0 (IBM, Chicago, IL, USA), with a significantly different set with $p < 0.05$. A structural equation model (SEM) was used to distinguish the direct and indirect influence of soil moisture on SOC content. The fitness of the model was evaluated based on the following criteria: X/df < 2, $p > 0.05$, root mean square error of approximation <0.07 and goodness-of-fit index (GFI) > 0.9 (Hooper, Coughlan, & Mullen, 2008). The SEM was conducted using the Amos 20.0 software program (Amos Development Corporation, Crawfordville, FL, USA).

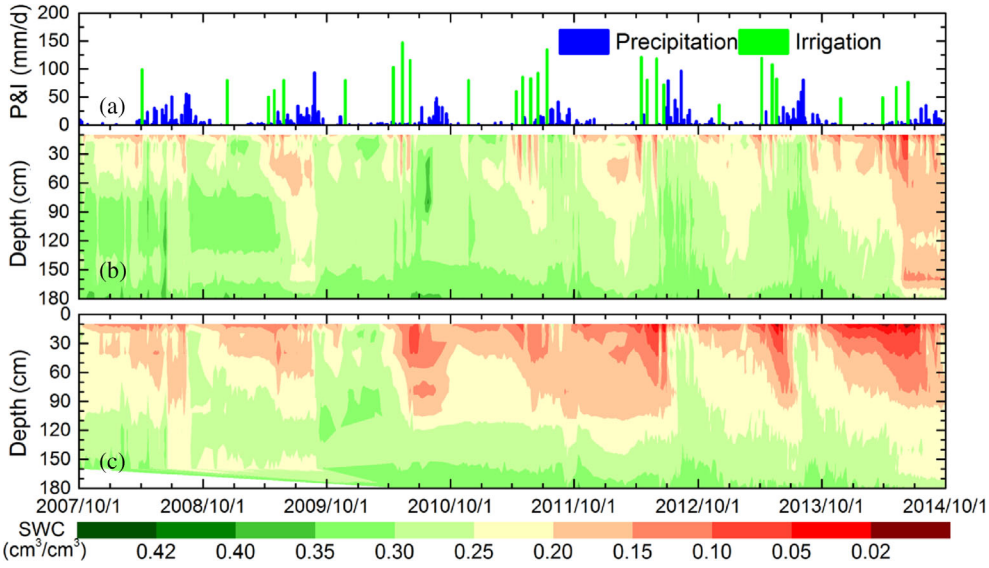

FIGURE 1 (a) Precipitation and irrigation (mm d^{-1}), and soil water content in (b) irrigation and (c) non-irrigation plots at different depths from 2007 to 2014

TABLE 1 Soil properties in irrigation and non-irrigation plots during different sampling times

Treatment	Sampling time	Soil pH	Soil moisure (%)	SOC (g kg^{-1})	Soil available N (mg kg^{-1})	Soil available P (mg kg^{-1})
Irrigation	April 2013	7.8 ± 0.06	8.7 ± 0.2	9.4 ± 0.1	74.9 ± 5.6	55 ± 11
	May 2013	8.1 ± 0.03	18.5 ± 0.2	9.1 ± 0.1	72.9 ± 3.4	39 ± 4
	October 2013	7.8 ± 0.07	15.4 ± 1.5	10.5 ± 0.3	78.8 ± 4.8	94 ± 7
	November 2013	7.8 ± 0.05	13.1 ± 0.5	9.5 ± 0.4	71.0 ± 2.6	91 ± 6
	April 2014	7.7 ± 0.05	14.6 ± 0.2	10.3 ± 0.4	78.4 ± 3.5	30 ± 2
	June 2014	8.1 ± 0.03	5.5 ± 0.2	8.8 ± 0.4	63.2 ± 6.1	43 ± 7
	July 2014	7.7 ± 0.05	11.2 ± 0.9	10.1 ± 0.2	78.9 ± 4.4	25 ± 3
Non-irrigation	April 2013	7.8 ± 0.06	6.4 ± 0.5	9.8 ± 0.2	70.5 ± 3.2	48 ± 4
	May 2013	8.2 ± 0.03	4.3 ± 0.1	9.8 ± 0.4	66.6 ± 0.8	46 ± 4
	October 2013	7.8 ± 0.01	14.2 ± 0.6	10.8 ± 0.4	76.6 ± 2.7	89 ± 7
	November 2013	7.8 ± 0.04	11.0 ± 0.2	10.4 ± 0.2	73.8 ± 3.6	83 ± 6
	April 2014	7.4 ± 0.06	5.2 ± 0.1	10.5 ± 0.3	88.8 ± 5.4	31 ± 4
	June 2014	7.8 ± 0.03	4.7 ± 0.3	9.3 ± 0.3	69.4 ± 0.9	42 ± 2
	July 2014	7.6 ± 0.02	7.6 ± 0.3	10.2 ± 0.2	81.9 ± 7.6	30 ± 6
Treatment effect	Irrigation	$p < 0.01$	$p < 0.001$	$p < 0.05$	$p < 0.05$	$p < 0.05$
	Time	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.01$	$p < 0.001$
	I × T	$p < 0.01$	$p < 0.001$	$p < 0.05$	$p < 0.05$	$p < 0.05$

Note: The effects of irrigation on soil properties were tested by two-way repeated-measured ANOVA with sampling time and irrigation treatment as factors. Values represent means ± standard errors. SOC, soil organic carbon; N, nitrogen; P, phosphorus

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3 | RESULTS

3.1 | Effects of irrigation on soil properties

The precipitation at our field station varied over seven experimental years (Figure 1). The precipitation was particularly low in 2010 and 2011, resulting in stronger low moisture in that period (Figure 1a). Soil water content (SWC) in the non-irrigation treatments was generally lower than in the irrigation over the 7 years (Figure 1b,c).

In this experiment, irrigation significantly increased the soil moisture content by 38% and decreased the SOC concentration by 4.2% ($p < 0.05$; Table 1), whereas the available soil N and P were not affected by the irrigation ($p > 0.05$; Table 1). All abiotic soil properties measured in this study were strongly affected by sampling time, showing variations among sampling times ($p < 0.05$; Table 1). In addition, soil pH was significantly influenced by both the irrigation and sampling time ($p < 0.05$; Table 1).

3.2 | Effects of irrigation on soil microbial community composition

The fungal biomass significantly decreased after irrigation and varied with sampling time ($p < 0.05$; Figure 2a).

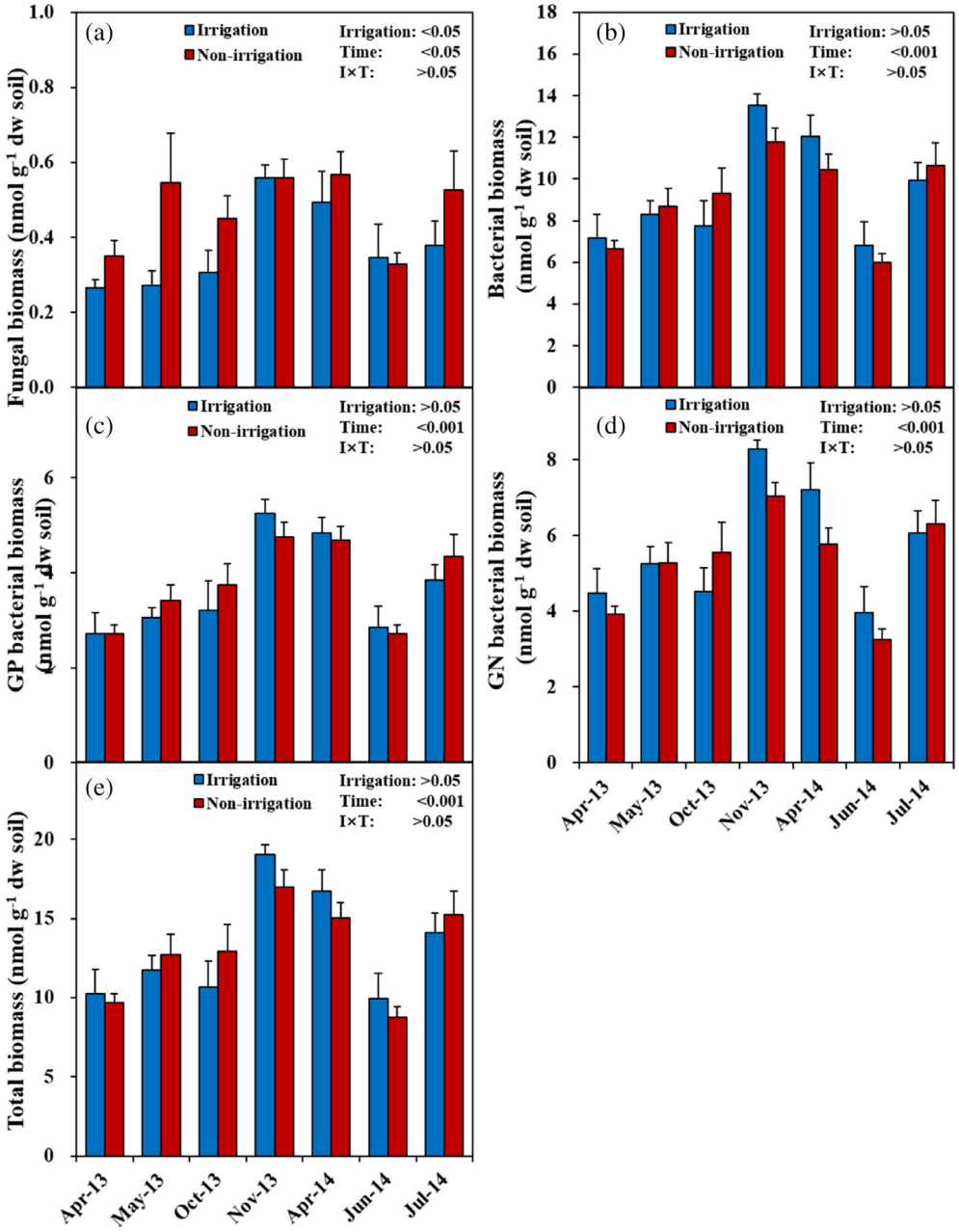

FIGURE 2 Fungal (a), bacterial (b), Gram-positive (GP) bacterial (c), Gram-negative (GN) bacterial (d) and total microbial (e) biomass (represented by phospholipid fatty acid (PLFA) abundance) in irrigation and non-irrigation plots across different sampling times

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Under non-irrigation treatments, the total microbial, bacterial, Gram-positive bacterial and Gram-negative bacterial biomass all stayed at a similar level to non-irrigation across sampling times ($p > 0.05$; Figure 2b–e). Sampling time significantly affected the biomass of different microbial groups ($p < 0.05$; Figure 2). The ratio of fungal to bacterial PLFA abundance and the ratio of Gram-positive-to-Gram-negative bacterial PLFA abundances decreased by 30% and 10%, respectively, in the irrigation treatment compared with non-irrigation across sampling time ($p < 0.001$; Figure 3).

Results from the multivariate dimensionality reduction analysis showed that the relative abundance of PLFA biomarkers distinctly differed between the irrigation and non-irrigation treatments. The effect of soil properties explained 27.7% in axis 1 and 5.4% in axis 2 of the microbial PLFA biomarker abundances, and soil moisture showed the strongest effect among all soil properties (Figure 4).

3.3 | The effect of irrigation on the relationship between soil microbial community and soil organic carbon content

We used a structural equation model (SEM) to assess the extent of the direct or indirect influence of soil moisture on SOC concentration (Figure 5). The fitted models met the significance criteria ($\chi^2/df = 0.24$, $p = 0.88$). Total microbial biomass, soil physicochemical index (including available N, available P and pH) and the ratio of microbial group changes explained 39% of the variation in SOC concentration. Soil moisture contributed most to the increased SOC concentration by influencing the ratio of soil fungal-to-bacterial PLFA abundance among all variables, whereas the ratio of Gram-positive-to-Gram-negative bacterial PLFA abundance showed no significant effect on SOC concentration (Figure 5). In addition, soil moisture, soil physicochemical index and total microbial

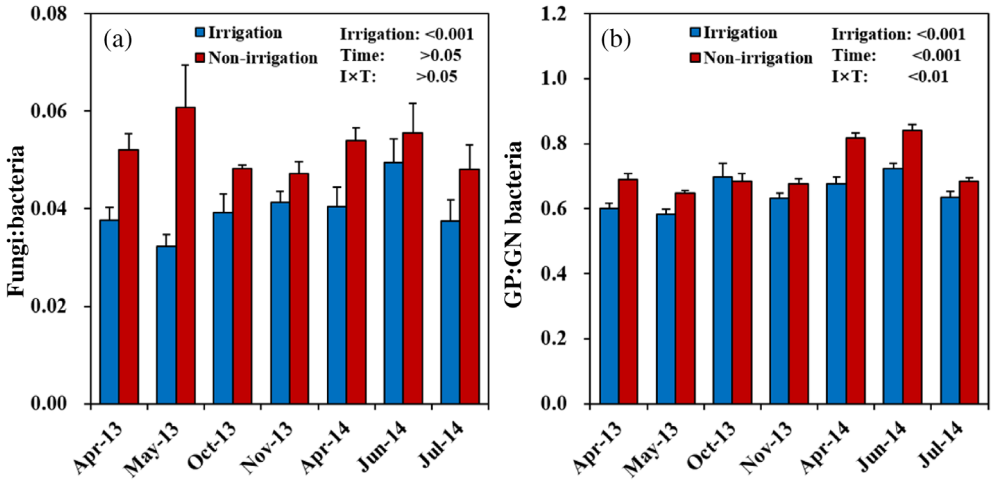

FIGURE 3 Fungal:bacterial phospholipid fatty acid (PLFA) ratio (a) and Gram-positive (GP):Gram-negative(GN) bacterial PLFA ratio (b) in irrigation and non-irrigation plots across different sampling times

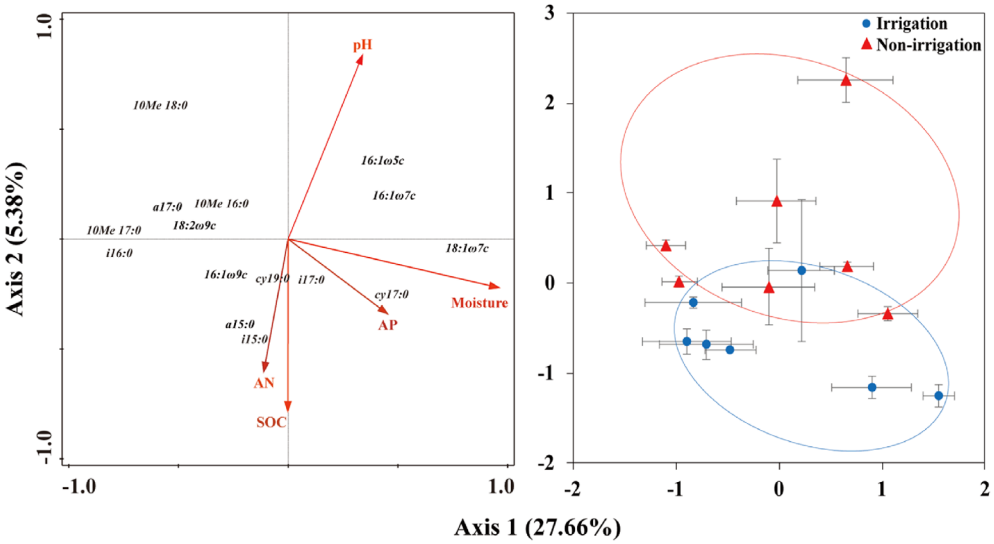

FIGURE 4 Multivariate dimensionality reduction analysis of the irrigation effect on microbial phospholipid fatty acid (PLFA) biomarker abundance across different sampling times

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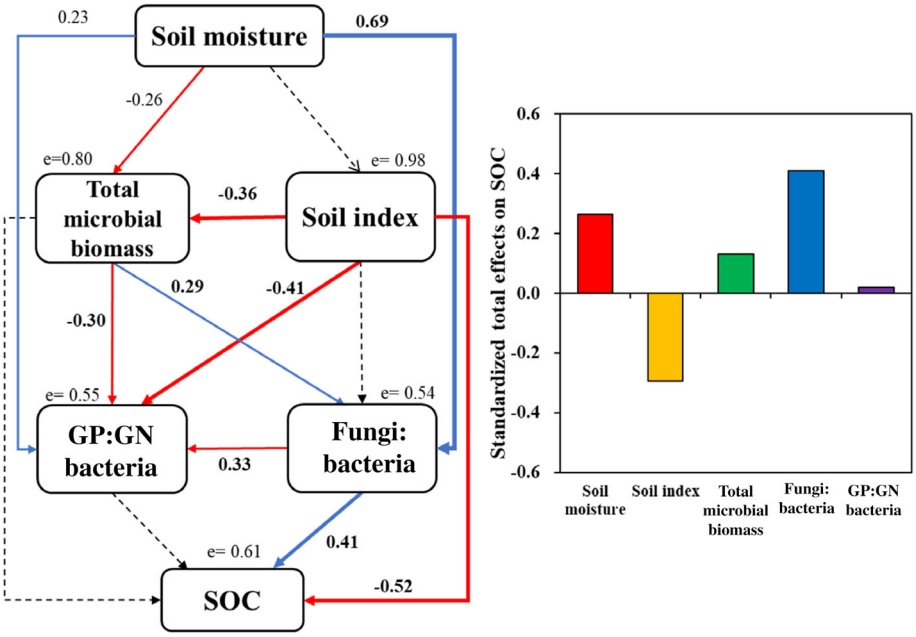

FIGURE 5 Structural equation model showing the hypothesized causal relationships among soil moisture, soil physicochemical index (soil availability N, P and soil pH), total microbial biomass, fungi-to-bacteria ratio and Gram-positive (GP) to Gram-negative (GN) bacteria ratio effect on the soil organic carbon (SOC) content. The width of the arrow represents the strength of the standardized path coefficient. Continuous arrows indicate significant relationships, whereas dashed arrows indicate no significant relationship. The e value indicates residual. Standardized total effects (direct plus indirect effects) from the model (right panel) indicate the effect size of the relationship

biomass all showed direct or indirect influences on SOC concentration (Figure 5).

4 | DISCUSSION

In our study area, the rainfall is not sufficient for the rapid growth of the vegetation, especially during the dry, windy spring season. Therefore, intensive irrigation regimes have long been imposed to relieve drought stress in agriculture in this region (Xiao & Tao, 2014). Our results demonstrated that 7-year irrigation strongly influenced soil microbial community composition, and hence affected the soil carbon content in the semiarid agroecosystem.

4.1 | The response of soil microbial community composition to irrigation

Soil microbial community composition can be strongly affected by soil moisture (Frindte, Pape, Werner, Loeffler, & Knief, 2019). Our results showed that irrigation strongly increased soil moisture during the 7 years. Accordingly, we found that irrigation significantly affected the ratios of different microbial groups and the PLFA biomarker abundances. These results support our first hypothesis that the ratio between fungi and bacteria decreased after long-term irrigation, and was dependent on sampling time in a semiarid agroecosystem.

Although the total microbial biomass was not affected by irrigation, both fungal biomass and the ratio of fungal-to-bacterial PLFA abundance were significantly decreased under irrigation. This was consistent with previous studies showing that fungi are more tolerant than bacteria to drought in both laboratory and field experiments (de Vries et al., 2018; Preece et al., 2019). Fungal chitinous cell walls make them more resistant to drought, and their hyphal networks may benefit the growth of fungi and allow them to acquire more water and nutrients over long distances in low-moisture environments (de Boer et al., 2005; Guggenberger et al., 1999). Furthermore, soil moisture can affect both the quantity and composition of root exudates, and these exudates may strongly influence the microbial community via labile carbon, signalling molecules and phytohormones (de Vries, Griffiths, Knight, Nicolitch, & Williams, 2020; Fuchslueger et al., 2014; Lei et al., 2020; Li, Zhou, Alaei, & Bengtson, 2020). Indeed, a field study has demonstrated that low soil moisture content reduces plant-assimilated carbon acquired by bacteria, but does not influence carbon transfer to fungi (Fuchslueger et al., 2014).

In contrast to our hypothesis, both Gram-positive and Gram-negative bacterial biomass did not significantly differ between irrigation and non-irrigation treatments. However, we found that the microbial community differed after irrigation, and the ratio of Gram-positive to Gram-negative bacterial PLFA abundance in the non-irrigation treatment was higher than that in the irrigation treatment. The lower ratio of Gram-positive bacteria-to-Gram-negative bacteria in the irrigation treatment may be caused by differences in cell-wall structure and physiological functioning between the two bacterial groups (Canarini et al., 2016). Gram-positive bacteria are

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generally more resistant to drought due to their cell wall composition and are classified as "drought-adapted generalists" (Manzoni, Schimel, & Porporato, 2012; Schimel, Balser, & Wallenstein, 2007). Gram-positive bacteria are also more complex substrates and potentially have a more advanced osmoregulatory strategy than Gram-negative bacteria (Harris, 1981). Moreover, the capacity of many Gram-positive bacteria to sporulate allows them to withstand a variety of disturbances, including lower soil moisture (Drenovsky et al., 2010). In summary, the above microbial survival strategies offer a possible explanation for the variation in the ratios between different bacterial groups after irrigation. Similar results have been found in other studies showing that variation of soil moisture can strongly influence the bacterial community biomass or diversity (Alster, German, Lu, & Allison, 2013; Fuchslueger et al., 2014; Sheik et al., 2011).

4.2 | Irrigation effect on the soil C storage and its linkage with soil microbial community composition

Cycling of soil carbon strongly depends on soil environmental factors, such as soil water content (Condron, Hopkins, Gregorich, Black, & Wakelin, 2014; Lei et al., 2016; Lei et al., 2020). In our experimental period, the non-irrigation treatment significantly increased SOC concentration compared with the irrigation treatment. Other studies also reported that a low soil moisture content reduces SOM mineralization and increases soil carbon content (Borken & Matzner, 2009; Larsen et al., 2011). Low water availability can limit SOM decomposition processes by decreasing microbial activity (Hueso et al., 2012; Zeglin et al., 2013), as well as decreasing the mobility of nutrients and energy sources, in return, resulting in a low substrate supply to microbial decomposers and nutrient limitation (Suseela, Conant, Wallenstein, & Dukes, 2012). In addition, there was more crop biomass in the irrigation treatment than in the non-irrigation treatment. Greater crop biomass would increase the carbon input into the soil from plants (e.g., root residues and exudation). The greater carbon input from plants would also result in variation of the microbial community, and induce rhizosphere priming, which might increase the SOM decomposition rate, by up to 380% (Cheng et al., 2014; Li, Alaei, Zhou, & Bengtson, 2021).

Soil carbon content is directly and indirectly affected by the soil microbial community dynamics, microbial activity and microbial decomposition (Six, Frey, Thiet, & Batten, 2006). We found that the ratio of soil fungal-to-bacterial PLFA abundance greatly contributed to the increased SOC concentration based on the SEM. Our result is consistent with reports that the fungal biomass showed a relative increase under low soil moisture content because fungi are better adapted to low-moisture conditions (Bapiri, Bååth, & Rousk, 2010; Barnard, Osborne, & Firestone, 2015; Preece et al., 2019). The variation in soil physical conditions by moisture availability might lead to soil carbon stabilization when the microbial community shifts towards a fungi-dominated community (Bardgett, Bowman, Kaufmann, & Schmidt, 2005; Manzoni et al., 2012). Soil fungal communities can sequester more carbon through a more recalcitrant cell-wall composition and higher carbon-use efficiency than those of bacteria (Bailey, Smith, & Bolton, 2002; Six et al., 2006). As observed in previous studies, a large population of fungi favours the formation of macroaggregates by the effect of their hyphae aggregating smaller aggregates into bigger ones, in which SOM is more resistant to decomposition than in microaggregates (Johnson, Gehring, & Jansa, 2016). Thus, soil carbon sequestration capacity would be more persistent when fungi dominate the microbial community, and the lower fungal biomass and ratio of fungal-to-bacterial abundance under irrigation would decrease soil carbon sequestration in the semiarid agroecosystem in the study area.

The bacterial community is strongly affected by soil water content in terms of their physiological status and SOM decomposition capacity, and different microbial groups generally show a different response to soil moisture content (Jansson & Hofmockel, 2020). Therefore, the bacterial community composition, for example, the ratio of Gram-positive-to-Gram-negative bacterial abundance, after soil moisture changes influences soil carbon content. Although there was a lower ratio of Gram-positive bacteria and Gram-negative bacteria in the non-irrigation than in the irrigation plots, our results show that the ratio of Gram-positive-to-Gram-negative bacterial biomass had no significant effect on the increased SOC concentration according to the SEM. This was probably due to neither the Gram-positive nor the Gram-negative bacterial biomass being significantly affected by the irrigation treatment. Moreover, the SEM analysis showed that the soil physicochemical index had a significant direct effect on the SOC concentration, but its residual value was high in the model and not caused by irrigation. Our results demonstrate that soil microbes are associated with higher soil carbon content through changes in microbial community composition in the semiarid agricultural ecosystems.

5 | CONCLUSIONS

Using a 7-year irrigation experiment, we found that irrigation significantly decreased soil carbon content of the

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topsoil (0–20 cm). Irrigation also, directly and indirectly, affected soil abiotic properties and influenced the soil microbial community composition, decreasing the fungal community and soil carbon content in the semiarid agroecosystem. Overall, our experiment demonstrates that (a) the responses of soil microbial communities to irrigation were highly taxa dependent and the groups adapted to low availability of water such as the fungi-dominated group were not favoured; (b) irrigation could influence soil carbon sequestration through its effect on the ratio between bacteria and fungi. These findings allow us to predict the response of soil carbon content in a semiarid agroecosystem to future climate change.

ACKNOWLEDGEMENTS

Liu Z.F. was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (No. XDB40020203) and the National Natural Science Foundation of China (No. 41771278). Qi Y.Q. was supported by the National Natural Science Foundation of China (No. 41930865 and No. 41001060). D.H. was supported by the US National Science Foundation (NSF) projects. J.P. and J.S. would like to acknowledge the financial support from the European Research Council Synergy grant ERC-SyG-2013-610028 IMBALANCE-P.

CONFLICT OF INTEREST

The authors declare they have no conflict of interests.

AUTHOR CONTRIBUTIONS

Conceptualization; investigation; writing - original draft. **Jian Li:** Formal analysis; investigation; writing - original draft. **Shaojun Deng:** Formal analysis; writing-review & editing. **Jun Wang:** Investigation; writing-review &-editing. **Yanju Zhang:** Formal analysis; investigation. **Hongwei Pei:** Data curation; visualization. **Yanjun Shen:** Project administration; writing-review & editing. **Dafeng Hui:** Writing-review & editing. **Hans Lambers:** Writing-review & editing. **Jordi Sardans:** Writing-review & editing. **Josep Peñuelas:** Writing-review & editing. **Zhanfeng Liu:** Conceptualization; funding acquisition; writing - original draft.

DATA AVAILABILITY STATEMENT

Data will be supplied as supporting information.

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REFERENCES

Alster, C. J., German, D. P., Lu, Y., & Allison, S. D. (2013). Microbial enzymatic responses to drought and to nitrogen addition in a southern California grassland. *Soil Biology and Biochemistry*, *64*, 68–79.

Bailey, V. L., Smith, J. L., & Bolton, H. (2002). Fungal-to-bacterial ratios in soils investigated for enhanced C sequestration. *Soil Biology and Biochemistry*, *34*, 997–1007.

Bapiri, A., Bååth, E., & Rousk, J. (2010). Drying-rewetting cycles affect fungal and bacterial growth differently in an arable soil. *Microbial Ecology*, *60*, 419–428.

Bardgett, R. D., Bowman, W. D., Kaufmann, R., & Schmidt, S. K. (2005). A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology and Evolution*, *20*, 634–641.

Bardgett, R. D., Freeman, C., & Ostle, N. J. (2008). Microbial contributions to climate change through carbon cycle feedbacks. *The ISME Journal*, *2*, 805–814.

Barnard, R. L., Osborne, C. A., & Firestone, M. K. (2013). Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *The ISME Journal*, *7*, 2229–2241.

Barnard, R. L., Osborne, C. A., & Firestone, M. K. (2015). Changing precipitation pattern alters soil microbial community response to wet-up under a Mediterranean-type climate. *The ISME Journal*, *9*, 946–957.

Borken, W., & Matzner, E. (2009). Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology*, *15*, 808–824.

Bruun, S., Clauson-Kaas, S., Bobulska, L., & Thomsen, I. K. (2014). Carbon dioxide emissions from biochar in soil: Role of clay, microorganisms and carbonates. *European Journal of Soil Science*, *65*, 52–59.

Canarini, A., Carrillo, Y., Mariotte, P., Ingram, L., & Dijkstra, F. A. (2016). Soil microbial community resistance to drought and links to C stabilization in an Australian grassland. *Soil Biology and Biochemistry*, *103*, 171–180.

Cheng, W. X., Parton, W. J., Gonzalez-Meler, M. A., Phillips, R., Asao, S., McNickle, G. G., ... Jastrow, J. D. (2014). Synthesis and modeling perspectives of rhizosphere priming. *New Phytologist*, *201*, 31–44.

Chodak, M., Golebiewski, M., Morawska-Ploskonka, J., Kuduk, K., & Niklinska, M. (2015). Soil chemical properties affect the reaction of forest soil bacteria to drought and rewetting stress. *Annals of Microbiology*, *65*, 1627–1637.

Condron, L. M., Hopkins, D. W., Gregorich, E. G., Black, A., & Wakelin, S. A. (2014). Long-term irrigation effects on soil organic matter under temperate grazed pasture. *European Journal of Soil Science*, *65*, 741–750.

de Boer, W., Folman, L. B., Summerbell, R. C., & Lynne, B. (2005). Living in a fungal world: Impact of fungi on soil bacterial niche development. *FEMS Microbiology Reviews*, *29*, 795–811.

de Deyn, G. B., Quirk, H., Oakley, S., Ostle, N., & Bardgett, R. D. (2011). Rapid transfer of photosynthetic carbon through the plant-soil system in differently managed species-rich grasslands. *Biogeosciences*, *8*, 1131–1139.

de Vries, F. T., Griffiths, R. I., Bailey, M., Craig, H., Girlanda, M., Gweon, H. S., ... Bardgett, R. D. (2018). Soil bacterial networks are less stable under drought than fungal networks. *Nature Communications*, *9*, 3033.

13652389, 2022, 1, Downloaded from https://bsssjournals.onlinelibrary.wiley.com/doi/10.1111/ejss.13143 by National Cheng Kung University, Wiley Online Library on [10/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

de Vries, F. T., Griffiths, R. I., Knight, C. G., Nicolitch, O., & Williams, A. (2020). Harnessing rhizosphere microbiomes for drought-resilient crop production. *Science*, *368*, 270–274.

Drenovsky, R. E., Steenwerth, K. L., Jackson, L. E., & Scow, K. M. (2010). Land use and climatic factors structure regional patterns in soil microbial communities. *Global Ecology and Biogeography*, *19*, 27–39.

Du, Y.-D., Niu, W.-Q., Gu, X.-B., Zhang, Q., Cui, B.-J., & Zhao, Y. (2018). Crop yield and water use efficiency under aerated irrigation: A meta-analysis. *Agricultural Water Management*, *210*, 158–164.

Evans, S. E., Wallenstein, M. D., & Fierer, N. (2014). Climate change alters ecological strategies of soil bacteria. *Ecology Letters*, *17*, 155–164.

Frindte, K., Pape, R., Werner, K., Loeffler, J., & Knief, C. (2019). Temperature and soil moisture control microbial community composition in an arctic-alpine ecosystem along elevational and micro-topographic gradients. *The ISME Journal*, *13*, 2031–2043.

Frostegård, A., & Bååth, E. (1996). The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. *Biology and Fertility of Soils*, *22*, 59–65.

Fuchslueger, L., Bahn, M., Fritz, K., Hasibeder, R., & Richter, A. (2014). Experimental drought reduces the transfer of recently fixed plant carbon to soil microbes and alters the bacterial community composition in a mountain meadow. *New Phytologist*, *201*, 916–927.

Guggenberger, G., Frey, S. D., Six, J., Paustian, K., & Elliott, E. T. (1999). Bacterial and fungal cell-wall residues in conventional and no-tillage agroecosystems. *Soil Science Society of America Journal*, *63*, 1188–1198.

Harris, R. F. (1981). Effect of water potential on microbial growth and activity. *Water Potential Relations in Soil Microbiology*, *9*, 23–95.

Hooper, D., Coughlan, J., & Mullen, M. R. (2008). Structural equation modelling: Guidelines for determining model fit. *Electronic Journal of Business Research Methods*, *6*, 53–60.

Hueso, S., Garcia, C., & Hernandez, T. (2012). Severe drought conditions modify the microbial community structure, size and activity in amended and unamended soils. *Soil Biology and Biochemistry*, *50*, 167–173.

Jafarikouhini, N., Kazemeini, S. A., & Sinclair, T. R. (2020). Sweet corn nitrogen accumulation, leaf photosynthesis rate, and radiation use efficiency under variable nitrogen fertility and irrigation. *Field Crops Research*, *257*, 6.

Jansson, J. K., & Hofmockel, K. S. (2020). Soil microbiomes and climate change. *Nature Reviews: Microbiology*, *18*, 35–46.

Johnson, N. C., Gehring, C., & Jansa, J. (2016). *Mycorrhizal mediation of soil: Fertility, structure, and carbon storage*. Cambridge: Elsevier.

Jones, D. L., Nguyen, C., & Finlay, R. D. (2009). Carbon flow in the rhizosphere: Carbon trading at the soil–root interface. *Plant and Soil*, *321*, 5–33.

Kaisermann, A., Roguet, A., Nunan, N., Maron, P. A., Ostle, N., & Lata, J. C. (2013). Agricultural management affects the response of soil bacterial community structure and respiration to water-stress. *Soil Biology and Biochemistry*, *66*, 69–77.

Larsen, K. S., Andresen, L. C., Beier, C., Jonasson, S., Albert, K. R., Ambus, P., … Stevnbak, K. (2011). Reduced N cycling in response to elevated CO_2, warming, and drought in a Danish heathland: Synthesizing results of the CLIMAITE project after two years of treatments. *Global Change Biology*, *17*, 1884–1899.

Lei, T. J., Feng, J., Zheng, C. Y., Li, S. G., Wang, Y., Wu, Z. T., … Cheng, H. (2020). Review of drought impacts on carbon cycling in grassland ecosystems. *Frontiers of Earth Science*, *14*, 462–478.

Lei, T. J., Pang, Z. G., Wang, X. Y., Li, L., Fu, J., Kan, G. Y., … Shao, C. L. (2016). Drought and carbon cycling of grassland ecosystems under global change: A review. *Water*, *8*, 460.

Lesk, C., Rowhani, P., & Ramankutty, N. (2016). Influence of extreme weather disasters on global crop production. *Nature*, *529*, 84–87.

Li, J., Alaei, S., Zhou, M., & Bengtson, P. (2021). Root influence on soil nitrogen availability and microbial community dynamics results in contrasting rhizosphere priming effects in pine and spruce soil. *Functional Ecology*, *35*, 1312–1324.

Li, J., Zhou, M., Alaei, S., & Bengtson, P. (2020). Rhizosphere priming effects differ between Norway spruce (*Picea abies*) and scots pine seedlings cultivated under two levels of light intensity. *Soil Biology and Biochemistry*, *145*, 107788.

Lu, R. (1999). *Analytical methods of soil Agrochemistry*. Beijing, China: Chinese Agriculture Science and Technology Press.

Manzoni, S., Schimel, J. P., & Porporato, A. (2012). Responses of soil microbial communities to water stress: Results from a meta-analysis. *Ecology*, *93*, 930–938.

McHugh, T. A., & Schwartz, E. (2015). Changes in plant community composition and reduced precipitation have limited effects on the structure of soil bacterial and fungal communities present in a semiarid grassland. *Plant and Soil*, *388*, 175–186.

Nesci, A., Etcheverry, M., & Magan, N. (2004). Osmotic and matric potential effects on growth, sugar alcohol and sugar accumulation by *aspergillus section* Flavi strains from Argentina. *Journal of Applied Microbiology*, *96*, 965–972.

Preece, C., Verbruggen, E., Liu, L., Weedon, J. T., & Peñuelas, J. (2019). Effects of past and current drought on the composition and diversity of soil microbial communities. *Soil Biology and Biochemistry*, *131*, 28–39.

Punsalang, A., Healmbbs, J. M., & Murphy, P. J. (1989). Growth of gram-positive and gram-negative bacteria in platelet concentrates. *Transfusion*, *29*, 596–599.

Rousk, J., Bååth, E., Brookes, P. C., Lauber, C. L., Lozupone, C., Caporaso, J. G., … Fierer, N. (2010). Soil bacterial and fungal communities across a pH gradient in an arable soil. *The ISME Journal*, *4*, 1340–1351.

Rousk, J., Smith, A. R., & Jones, D. L. (2013). Investigating the long-term legacy of drought and warming on the soil microbial community across five European shrubland ecosystems. *Global Change Biology*, *19*, 3872–3884.

Ruehr, N. K., Offermann, C. A., Gessler, A., Winkler, J. B., Ferrio, J. P., Buchmann, N., & Barnard, R. L. (2009). Drought effects on allocation of recent carbon: From beech leaves to soil CO_2 efflux. *New Phytologist*, *184*, 950–961.

Schimel, J., Balser, T. C., & Wallenstein, M. (2007). Microbial stress-response physiology and its implications for ecosystem function. *Ecology*, *88*, 1386–1394.

Sheik, C. S., Beasley, W. H., Elshahed, M. S., Zhou, X., Luo, Y., & Krumholz, L. R. (2011). Effect of warming and drought on grassland microbial communities. *The ISME Journal*, *5*, 1692–1700.

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Six, J., Frey, S. D., Thiet, R. K., & Batten, K. M. (2006). Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Science Society of America Journal*, *70*, 555–569.

Sleator, R. D., & Hill, C. (2002). Bacterial osmoadaptation: The role of osmolytes in bacterial stress and virulence. *FEMS Microbiology Reviews*, *26*, 49–71.

Strickland, M. S., & Rousk, J. (2010). Considering fungal:bacterial dominance in soils-methods, controls, and ecosystem implications. *Soil Biology and Biochemistry*, *42*, 1385–1395.

Su, X., Su, X., Yang, S., Zhou, G., Ni, M., Wang, C., … Deng, J. (2020). Drought changed soil organic carbon composition and bacterial carbon metabolizing patterns in a subtropical evergreen forest. *Science of the Total Environment*, *736*, 139568.

Suberkropp, K., & Weyers, H. S. (1996). Application of fungal and bacterial production methodologies to decomposing leaves in streams. *Applied and Environmental Microbiology*, *62*, 1610–1615.

Suseela, V., Conant, R. T., Wallenstein, M. D., & Dukes, J. S. (2012). Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Global Change Biology*, *18*, 336–348.

Wang, G. Y., Hu, Y. X., Liu, Y. X., Ahmad, S., & Zhou, X. B. (2021). Effects of supplement irrigation and nitrogen application levels on soil carbon-nitrogen content and yield of one-year double cropping maize in subtropical region. *Water*, *13*, 14.

Wang, Y., Hao, Y., Cui, X. Y., Zhao, H., Xu, C., Zhou, X., & Xu, Z. (2014). Responses of soil respiration and its components to drought stress. *Journal of Soils and Sediments*, *14*, 99–109.

Xiao, D., Shen, Y., Zhang, H., Moiwo, J. P., Qi, Y., Wang, R., … Shen, H. (2016). Comparison of winter wheat yield sensitivity to climate variables under irrigated and rain-fed conditions. *Frontiers of Earth Science*, *10*, 444–454.

Xiao, D., & Tao, F. (2014). Contributions of cultivars, management and climate change to winter wheat yield in the North China plain in the past three decades. *European Journal of Agronomy*, *52*, 112–122.

Zeglin, L., Bottomley, P., Jumpponen, A., Rice, C., Arango, M., Lindsley, A., … Myrold, D. (2013). Altered precipitation regime affects the function and composition of soil microbial communities on multiple time scales. *Ecology*, *94*, 2334–2345.

Zelles, L. (1999). Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: A review. *Biology and Fertility of Soils*, *29*, 111–129.

Zhang, J., Chen, H., & Zhang, Q. (2019). Extreme drought in the recent two decades in northern China resulting from Eurasian warming. *Climate Dynamics*, *52*, 2885–2902.

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How to cite this article: Qi, Y., Li, J., Deng, S., Wang, J., Zhang, Y., Pei, H., Shen, Y., Hui, D., Lambers, H., Sardans, J., Peñuelas, J., & Liu, Z. (2022). Long-term irrigation reduces soil carbon sequestration by affecting soil microbial communities in agricultural ecosystems of northern China. *European Journal of Soil Science*, *73*(1), e13143. https://doi.org/10.1111/ejss.13143

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