Science of the Total Environment 756 (2021) 143899

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Bacteria are more sensitive than fungi to moisture in eroded soil by natural grass vegetation restoration on the Loess Plateau

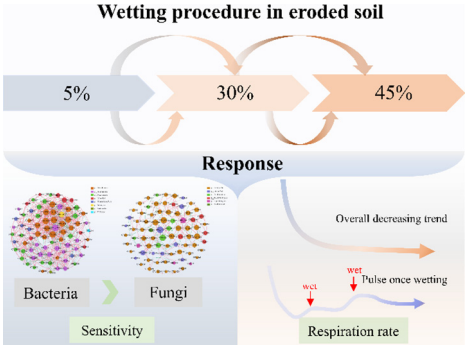
Panpan Jiao [a,b], Zhongwu Li [a,d,e,*], Lei Yang [b,c], Jijun He [f,**], Xiaofeng Chang [a], Haibing Xiao [g], Xiaodong Nie [d], Di Tong [e]

[a] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation CAS and MWR, Yangling 712100, China
[b] University of Chinese Academy of Sciences, Beijing 100000, China
[c] Key Laboratory of Soil Environment and Pollution Remediation, Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210008, China
[d] College of Resources and Environmental Sciences, Hunan Normal University, Changsha 410081, China
[e] College of Environmental Science and Engineering, Hunan University, Changsha 410082, China
[f] Base of the State Laboratory of Urban Environmental Processes and Digital Modeling, Key Laboratory of 3D Information Acquisition and Application, Ministry of Education, Capital Normal University, Beijing 100048, China
[g] College of Resources and Environment, Huazhong Agricultural University, Wuhan 430070, China

HIGHLIGHTS

- Bacteria were more sensitive than fungi to wetting procedures of 5–30%, 5–30–45% and 30–45%.
- Fungal communities exhibited difference between 5–30–45% wetting procedure and constant 45% SM.
- Effect of SM variation on bacterial co-occurrence network was larger than for fungi.
- A two-step continual wetting procedure caused a pulsed microbial respiration rate.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 11 August 2020
Received in revised form 17 November 2020
Accepted 18 November 2020
Available online 2 December 2020

Editor: Manuel Esteban Lucas-Borja

Keywords:
Soil moisture
Microbial community
Respiration rate
Nature grass revegetation
Co-occurrence network
Loess Plateau

ABSTRACT

Community composition and respiration rates of bacterial and fungal communities from grass-covered eroded soils of the Loess Plateau responded differently to constant and increasing soil moisture (SM) regimes. The soils were incubated with SM contents of 5%, 30%, and 45% and with wetting processes in the SM ranges from 5% to 30% (5–30%), from 5% to 30% to 45% (5–30–45%) and from 30% to 45% (30–45%); high-throughput sequencing and co-occurrence network analyses were applied to investigate the different responses of the bacterial and fungal communities to changed SM. Our results showed that bacteria were more sensitive than fungi to changes in SM. The dominant bacterial communities converted from *Actinobacterial* to *Proteobacteria* and *Acidobacteria* in 5–30–45% wetting procedure. *Firmicutes* preferred wet condition and exhibited slow resilience. However, no difference was observed for the *Chloroflexi* communities across any sample. The obvious difference in fungal composition was found between the wetting process of 5–30–45% and constant 45% SM. During the 5–30–45% procedure, the respiration rate was higher than that at 30–45% procedure after incubation for 24 days. The respiration rate in 5–30% procedure was lower than that of 5–30–45% process after incubation for 16–27 days. The larger effects on bacterial response than on fungi were verified in network analysis. Multiple stepwise regression analysis showed that 84.40% of the variation in bacterial richness and diversity as well as fungal diversity can

* Correspondence to: Z. Li, State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation CAS and MWR, Yangling 712100, China.
** Corresponding author.
E-mail addresses: lizw@hnu.edu.cn (Z. Li), hejiun_200018@163.com (J. He).

https://doi.org/10.1016/j.scitotenv.2020.143899

be explained by changes in soil respiration rate in response to wetting procedure. Understanding the response of difference between bacterial and fungal community composition, phylum-levels networks and respiration rate to changes in SM is essential for the management of plant-soil-water relationship in the ecosystem after natural vegetation restoration on the Loess Plateau.

1. Introduction

Soil erosion is widely recognized as one of the main threats to the Loess Plateau in China, where concentrated rainstorms during a narrow time interval (Fu et al., 2013), as well as high temperatures and evapotranspiration rates, having accelerated soil degradation dramatically (Zhang et al., 2016; Orgiazzi and Panagos, 2018). To eliminate soil erosion and restore the ecosystem of the Loess Plateau, agricultural land has been converted into vegetation land over the past few decades, and slopes greater than 15° were abandoned in favor of natural grass recovery without anthropogenic interference (Zhang et al., 2016). However, based on climate model predictions of intensified precipitation and hydrological cycling in arid and semi-arid regions, the significantly increased frequency of both long periods of drought and extreme rainfall events would be anticipated for the Loess Plateau, resulting in the frequent variation of soil moisture (SM) content (Piao et al., 2010; Evans and Wallenstein, 2012). Therefore, SM will play an increasingly important role in ecosystem regulation processes following vegetation restoration in the Loess Plateau of China.

Additionally, revegetation can strongly influence soil properties, through changing the spatial distribution of SM (Vivoni et al., 2008) and differences in consumption rates of SM across different vegetation types (Zhang and Shangguan, 2016). By controlling the diffusion of carbon sources and nutrients in aqueous solution (Hawkes et al., 2017; Ren et al., 2017) and the gas resources for microbial community (Banerjee et al., 2016), the SM content may greatly affect the soil microbial community diversity and/or composition. Some previous studies have suggested that fungal communities are more sensitive than bacterial communities to changing SM in vegetation ecosystems (Kaisermann et al., 2015; McHugh and Schwartz, 2016). However, other studies have observed bacteria to be more influenced by and even to benefit more from disturbance of SM in grassland ecosystems (Pesaro et al., 2004). Moreover, no differences among microbial communities were also found using different SM conditions in grassland (Griffiths et al., 2003). Thus, the responsive pattern of different soil microbes in grassland vegetation to SM is still controversial and lacks applicability to grassland restoration soil. In addition, soil microbial respiration has further been shown to be affected by the variation of SM, causing increased respiration in different types of land (Birch, 1959; Kim et al., 2012). Fungi was found to have lower microbial metabolic rate than bacteria generally for the slower biomass turnover rate (Deng et al., 2016), and the fungal richness was closely related to its respiration (Tong et al., 2020). Other studies illustrated the fungal respiration rate was high in dry condition for the higher resistance to drought and access to substrates by hyphal, while the pulse was observed for bacteria after rewetting from dry soil with faster bacterial growth rate and subsequent soil carbon (C) over mineralization (Canarini et al., 2017). However, some research indicated that rewetting did not induce over mineralization of soil C by bacteria and fungi in partly dried soil (Kaisermann et al., 2015; Das et al., 2019). The contradictory conclusion may be due to the different soil texture and historical soil environment, such as SM. Therefore, the correlative mechanism between moisture and the soil microbial community as well as its respiration pattern in grass vegetation recovery areas of eroded soil remains unclear.

Various research about the effects of SM on the microbial community and respiration have been based on the SM being fixed at a specific level (Carson et al., 2010) or immediate rewetting (Fierer et al., 2003). The responses of the differences between bacterial and fungal communities on dynamic SMs are still unclear, and the deep understanding of bacterial and fungal interspecies network and respiration under different SMs is important for the restoration of vegetation ecosystem. Comparison of the network structure between bacteria and fungi as well as different respiration rates under different variations of SM are helpful for deeper understanding of the relationship of plant-soil-water, which may provide new information about the influence of different SM levels and the feedback mechanisms of soil microbes in grass vegetation restoration areas of the Loess Plateau ecosystem. Next-generation sequencing technologies have recently offered new opportunities for studying belowground communities by profiling microbial composition at the species level (Zhang et al., 2016), and co-occurrence network analysis has proven powerful to study the different interactions between bacterial and fungal network structures (He et al., 2017). This information is beneficial for the manager to understand the long-term relationship of grass restoration, soil microbial communities, respiration and SM content for restoring ecosystem on the Loess plateau. Therefore, a systematic and deep understanding of the different responses of bacterial and fungal communities and respirations to different SMs is important to manage the plant-soil-water relationship during the vegetation restoration on the Loess Plateau.

Our objectives were to (i) evaluate the different responses of bacterial and fungal communities and diversities and their corresponding networks and metabolize to variations in SM in natural grass vegetation restorations of eroded soil and (ii) explore the differences between bacterial and fungal respiration rate in the process of constant levels versus wetting procedures across different SM levels. We hypothesized that (H1) bacterial diversity, community structure, respiration rate and co-occurrence network are more sensitive than those of fungi in response to variations in SM and that (H2) the gradual wetting procedure causes pulses in the respiration rate. To test our hypothesis, bacterial and fungal diversity, composition, network and respiration rate were investigated under different SM conditions, including constant and varying SM levels.

2. Materials and methods

2.1. Study site

The study site was located in the Wuliwan watershed (36°51′41.23″-36°52′50.87″N, 109°19′49.20″-109°21′46.46″E), in the hinterland of the Loess Plateau, which is situated in the vicinity of the city of Yan'an, Shanxi Province, China. The samples were collected at 36°51′47.56″N and 109°21′1.24″E, at an altitude of 1248.00 m. The climate of this area is semi-arid with average annual temperature of 8.8 °C and average annual precipitation of 510 mm, most of which occurs by means of short-duration and high-intensity storms during the summer months (mainly from July to September) (Ren et al., 2018). The annual frost-free period is approximately 157 days. The dominant soil is mainly Huangmian soil (Calcic Cambisols, FAO), which was developed on wind-deposited loess parent material. For the porous texture, poor water and fertilizer retention, imperfect development and weak cohesion features, the Huangmian soil is extremely susceptible to erosion (Xiao et al., 2016; Xu et al., 2020).

Since 1973, the Wuliwan watershed, an experimental site for the Institute of Soil and Water Conservation of the Chinese Academy of Science (CAS), has been subjected to revegetation to the control soil erosion problem. In particular, those slopes exceeding 15° were

transformed into forest or abandoned land for natural recovery. Thus, abandoned farmlands characterized by *Artemisia sacrorum* for natural recovery were selected.

2.2. Soil sampling and treatment

After removing the litter layer of the topsoil (approximately 1 cm), triplicate soil samples were taken using a soil auger with diameter of 5 cm at a depth of 0–15 cm. Fine roots and large rocks were carefully but immediately removed from the samples. Those parts of the soil samples to be used to determine physicochemical characteristics were air dried and stored at 4 °C. The other part of the soil samples, which was to be used for incubation, was sieved through 2-mm mesh and immediately transported to the laboratory for incubation.

2.3. Soil physicochemical properties

The samples of air-dried soils were crushed and sieved through 2-mm mesh. The soil pH was assayed with a digital pH meter using the ratio of 1:2.5 (w/v) of soil-to-water. The soil moisture (SM) was calculated gravimetrically and presented as the percentage of soil water to dry weight. Soil organic carbon (SOC) was measured by dichromate oxidation (Kalembasa and Jenkinson, 1973). Total nitrogen (TN) was measured using the Kjeldahl (Kjeldahl, 1883) method, while available nitrogen (AN) was determined using the alkali N proliferation method (Duan et al., 2016). Dissolved organic carbon (DOC) and soil dissolved organic nitrogen (DON) were calculated as described in literatures (Ren et al., 2016; Nie et al., 2018). Additionally, the soil particle sizes were analyzed using the MasterSizer 2000 method. Finally, microbial biomass carbon (MBC) was calculated depending on the chloroform-fumigation extraction method (Vance et al., 1987). All of the physicochemical properties are shown in Table S1 (Supplementary materials). The soil-water characteristic curve was measured using a high-speed refrigerated centrifuge (CR2G, Hitachi Ltd., Tokyo, Japan) (Fig. S2).

2.4. Soil incubation

The soils were incubated according to method reported in literature with some modification (Banerjee et al., 2016). Triplicate samples were prepared, each containing 50 g of homogeneous soil in a 250 ml glass bottle; the SM was adjusted to 5%, 30%, and 45% by adding sterile deionized water onto the surface, or the samples were kept in a ventilated place to dry. SM level was achieved by adjusting the gravimetric water content. All soil samples were randomly arranged and pre-incubated for 7 days at 25 °C in the dark to stabilize the microbial activity before varying or making static the soil water (Xiao et al., 2017). Including the pre-incubation, all jars were incubated in the dark at 25 °C for a total of 31 days at 1, 3, 5, 7, 8, 9, 10, 12, 16, 17, 20, 23, 24, 27 and 31 days, respectively (Fig. 1). The measured CO_2 emission on each sampling day was used to calculate the respiration rate for the corresponding day. CO_2 emissions were measured using a GC system equipped (Agilent Technologies 7890B) with a thermal conductivity detector, and three replications of empty glass bottles were incubated in the dark at 25 °C as controls. In addition, the respiration rate represents the CO_2 emissions rate of the corresponding day.

In the process of varying or making static the SM, water was added by weighing the soils. Specifically, for the wetting procedure of 5–30–45%, 5–30%, and constant 5% SM, the 9 replications were at first held in the initial static period of 5% SM; at 16 days, 3 replications were changed to 30% SM. Then, at 23 days, these 3 replications were again changed to 45% SM; meanwhile 3 replications previously held static were changed to 30% SM. The remaining 3 replications were kept static at 5% SM until the experiment was completed. The wetting procedure of 30–45% and constant 30% SM were conducted similar to the above procedure for the 5–30% range. The 6 replications were at first held in the initial static period of 30% SM, at 23 days, 3 replications were changed to 30% SM; meanwhile the remaining 3 replications were kept static at 30% SM until the experiment was finished. A 45% SM level was kept static as for comparison (Fig. 1). At the end of the experiment (at 31 days), all of the experimental units were destructively sampled by collecting 5 g of soil and freezing at −70 °C for microbial community analysis.

2.5. Determination of bacterial and fungal communities

Illumina MiSeq sequencing was applied to analyze the soil microbes. A sample of 16S rRNA was amplified using 338F (5′-barcode-ACTCCT ACGGGAGGCAGCAG-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-

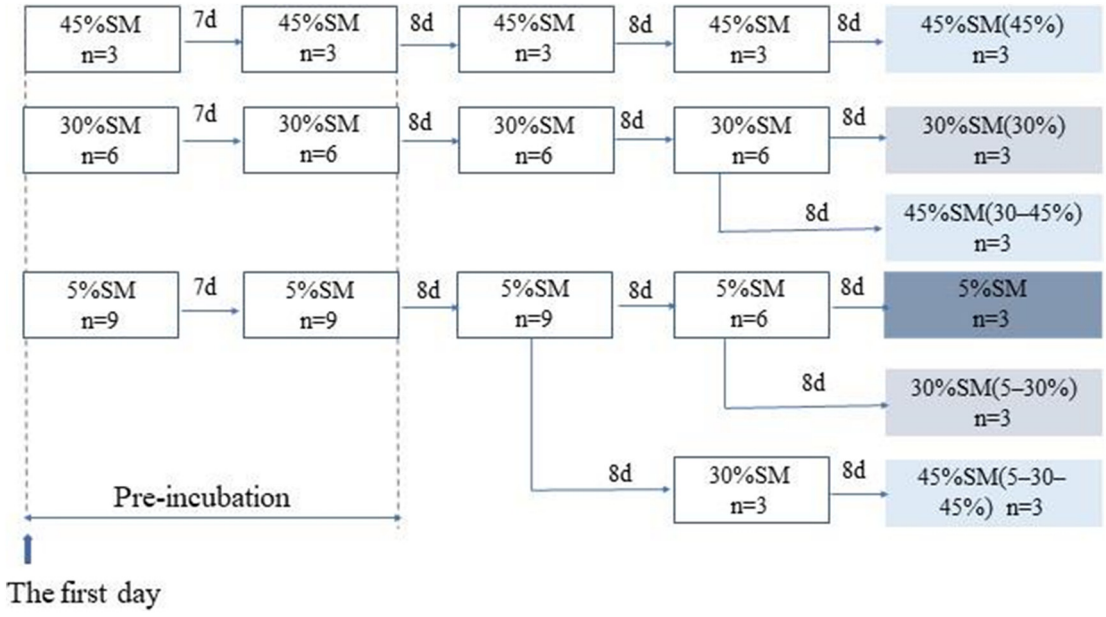


Fig. 1. Schematic presentation of the experimental design of soil moisture (SM) variation. Colored boxes represent that destructive sampling occurred. Each destructively sampled treatment was carried out in triplicate, and the measurement of CO_2 efflux occurred on days 1, 3, 5, 7, 8, 9, 10, 12, 16, 17, 20, 23, 24, 27 and 31.

3′) under the following conditions: denaturation at 95 °C for 10 min, followed by 40 cycles of 95 °C for 15 s, 55 °C for 60 s and 72 °C for 90 s, and finally being held at 72 °C for 7 min (Xiao et al., 2017; Tong et al., 2020). Moreover, ITS was amplified using ITS1-F (CTTGGTCATTTAGAGGAAGTAA) and ITS2 (GCTGCGTTCTTCATCGATGC) under the following conditions: denaturation at 95 °C for 5 min, followed by 35 cycles consisting of 1 min at 95 °C, 45 s at 53 °C and 1 min at 72 °C (Wang et al., 2019). The data for the purified PCR was obtained from an Illumina MiSeq PE250 platform (Illumina Corporation, USA). Operational taxonomic units (OTUs) were clustered at a 97% similarity threshold via UPARSE (version 7.1), and the screened sequences were obtained from the raw fastq files that were demultiplexed and quality-filtered by 'Quantitative Insights into Microbial Ecology' (QIIME version 1.8.0). Relative abundance was determined based on the number of OTUs affiliated with the same phylogenetic group divided by the total number of OTUs. In addition, the alpha diversity and richness of the microbial community were assessed by Shannon and Chao1 indices. The original reads were deposited into the NCBI Sequence Read Archive database with accession number SUB7902263.

2.6. Statistical analysis

One-way ANOVA was performed to analyze the differences across the different SM values followed by a least significance difference (LSD) test. Lists of the top 80 phyla of bacterial and fungal from the different SM values were each generated. Co-occurrence networks were explored and visualized with the interactive platform Gephi (https://gephi.github.io/), and the numbers of nodes and edges, network diameter, average degree, average weight degree, density, average clustering coefficient, average path length and modularity were calculated to describe the topological properties of the network (Gao et al., 2020). Moreover, multiple stepwise linear regression analysis was performed to determine the contributions of biotic properties to variations in microbial respiration rates in the different SM levels. In general, 6 biotic elements, including the bacterial and fungal Shannon diversity index (alpha diversity), Chao 1 (species richness), and PCAs (beta diversity), were chosen. All statistical analyses were calculated using the SPSS 23.0 software package (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Changes in soil microbial abundance and diversity

Bacterial OTUs in the constant 30% and 45% SM were 3180 and 3110 ($p > 0.05$), respectively, which were higher than that in constant 5% SM (2578, $p < 0.05$). The species richness (Chao 1) of the bacteria were significantly increased from 3429 to 4283 with the rise in constant 5% SM to 30% SM before decreasing to 4129 with SM being further increased to 45% ($p < 0.05$). Shannon index in constant 30% SM was 10.00, while that in constant 5% and 45% SM were different to be 9.48 and 9.77 respectively ($p < 0.05$). With the wetting procedure being extended from 30–45% to 5–30–45%, bacterial OTUs, species richness and Shannon index decreased significantly from 3151 to 2843, 4153 to 3972 and 9.86 to 9.55, respectively ($p < 0.05$). Similarly, bacterial OTUs, species richness and Shannon index for the wetting process of 5–30% were significantly lower than that for the constant 30% SM ($p < 0.05$). In addition, the OTUs and Shannon index for wetting process of 5–30% and for constant 5% were similar (2578 vs 2673 and 9.48 vs 9.48, $p > 0.05$), except for species richness ($p < 0.05$). When the SM was further increased to 45% after the 5–30–45% wetting procedure, OTUs and species richness were significantly higher than those for the constant 5% SM (i.e. 2843 vs 2578 for OTUs, and 3972 vs 3429 for species richness, respectively). However, comparing the wetting procedure of 30–45% and situation of constant SM being 30% or 45%, there were no obvious difference in the OTUs, species richness and Shannon index ($p > 0.05$) (Table 1).

The fungal OTUs in constant SM levels of 45% and 30% were similar (734 for 45% SM vs 780 for 30% SM, $p > 0.05$), which were remarkably lower than that in the constant 5% SM (922, $p < 0.05$). Fungal species richness in the constant 45% SM was significantly lower than that in constant 5% SM (1009 vs 1213, $p < 0.05$). The OTUs of fungi after wetting procedures of 5–30–45%, 30–45% and 5–30% exhibited no obvious difference to be about 870, which was significantly higher than 734 for the constant 45% and 780 for the constant 30% SM levels ($p < 0.05$). Similarly, the fungal species richness after wetting procedures of 5–30–45%, 30–45% and 5–30% were not different to be approximately 1200, which were not significantly different from those in constant SM of 30% and 5%, but obviously higher than that for constant 45% SM (1009, $p < 0.05$). However, significant difference existed between wetting process of 5–30–45% and constant SM of 45% for the Shannon index (6.31 vs 6.61, $p < 0.05$). In addition, no obvious difference was observed for Shannon index between other wetting processes and conditions of constant SMs ($p > 0.05$) (Table 1).

3.2. Changes in the soil microbial community composition

The overall composition of the soil microbial communities under constant and wetting regimes were analyzed with PCAs. PC1 and PC2 explained 32.48% and 12.48% of the variability for the bacterial community and explained 19.94% and 12.28% of the variability for the fungal community, respectively (Fig. S1a and b).

The relative abundances of specific bacteria were analyzed at the phylum level, and the dominant taxa were *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Bacteroidetes* and *Firmicutes*, which occupied 89.60–95.54% of the OTUs under conditions with different SM levels (Fig. 2a). *Actinobacteria* members were most abundant at the constant 5% SM level, accounting for 37.03% of the OTUs, and their abundance decreased sharply to 20.31% and 26.56% after the 5–30–45% and 5–30% wetting procedures, respectively ($p < 0.05$). Despite declining, these abundances were still remarkably higher than those under SM levels of constant 45% (11.53%), constant 30% (21.88%) and wetting process of 30–45% (13.28%) ($p < 0.05$).

Table 1
Microbial abundance and diversity indices under the different soil moisture (SM) conditions, including SM being held constant at 5%, 30% and 45% levels, wetting procedures with SM increasing from 30% to 45% (i.e., 30–45%) as well as with SM of 5–30% and 5–30–45%. Different letters in the same column indicate significant differences at the $p < 0.05$ level based on one-way ANOVA. OTUs: operational taxonomic units.

Treatment SM (%)	Bacteria						Fungi					
	OTUs		Chao1		Shannon index		OTUs		Chao1		Shannon index	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
45	3110a	78	4129ab	101	9.77bc	0.27	734c	80	1009b	161	6.61a	0.25
30–45	3151a	33	4153a	70	9.86ab	0.02	870ab	69	1188a	70	6.54ab	0.14
30	3180a	23	4283a	25	10.00a	0.06	780bc	15	1061ab	24	6.28bc	0.16
5	2578c	48	3429d	54	9.48d	0.08	922a	19	1213a	51	6.33bc	0.14
5–30	2673c	46	3715c	145	9.48d	0.06	870ab	58	1213a	113	6.27c	0.06
5–30–45	2843b	72	3972b	101	9.55cd	0.09	871a	20	1198a	21	6.31bc	0.05

Under the constant 5% SM level, the relative abundances of *Proteobacteria*, *Acidobacteria*, *Gemmatimonadetes* and *Bacteroidetes* were obviously lower than those in the constant SM levels of 30% and 45% or the wetting procedure of 5–30%, 5–30–45%, 30–45% SM levels ($p < 0.05$). Additionally, the relative abundances of *Proteobacteria*, *Gemmatimonadetes* and *Bacteroidetes* were obvious lower in the wetting procedure of 30–45% and 5–30–45% than those under the constant 45% SM, with the same trend observed for the comparison between 5–30% wetting process and the constant 30% SM ($p < 0.05$). *Firmicutes* was most abundant in constant 45% SM, with the abundance (6.93%) much higher than that in other SM levels ($p < 0.05$). The abundance of *Proteobacteria* and *Acidobacteria* was abruptly increased after the wetting procedure 5–30% and 5–30–45%, compared with that under the constant 5% SM. Similarly, the relative abundance of *Acidobacteria* was obviously increased after the wetting procedure 30–45%, compared with that under the constant 30% SM, while the decline trend was observed for the relative abundance of *Gemmatimonadetes* and *Bacteroidetes* ($p < 0.05$). No obvious difference was detected in *Chloroflexi* across all samples ($p > 0.05$) (Figs. 2a and 3a).

Furthermore, at the order level for bacterial community, the relative abundances of *Solirubrobacterales* and *Acidimicrobiales* decreased, and that of *Xanthomonadales* increased significantly with the constant SM being increased from 5% to 45%. After the wetting procedure of 5–30–45%, the relative abundance for *Sphingomonadales*, *Solirubrobacterales*, *Gaiellales* and *Acidimicrobiales* was significantly increased, and that of *Xanthomonadales* decreased compared with the situation for the constant SM level of 45% ($p < 0.05$). Meanwhile, the similar trend was observed in the wetting procedure of 5–30% when comparing with the constant 30% SM, except for *Gaiellales* and *Acidimicrobiales*. Conversely, compared with the constant 30% SM, the relative abundance of *Blastocatellales* was increased by 72.28% and those of *Solirubrobacterales*, *Gemmatimonadales*, *Gaiellales*, *Acidimicrobiales*, and *Sphingobacteriales* were decreased by 42.51%, 28.39%, 40.91%, 45.60% and 23.28%, respectively after the wetting procedure of 30–45% ($p < 0.05$) (Figs. 2b and 4a).

The dominant fungal phyla were *Ascomycota*, *Mortierellomycota*, *Basidiomycota*, *Chytridiomycota*, *Cercozoa*, *Rozellomycota* and they accounted for 85.14–92.45% of the OTUs in the different SM conditions (Fig. 2c). The wetting procedure of 5–30% or 5–30–45% enhanced the relative abundance of *Mortierellomycota* and but adversely affected that of *Basidiomycota* in comparison with constant 30% or 45% SM, respectively. The relative abundance of *Ascomycota* was decreased by 12.04% in the wetting procedure of 5–30–45% when comparing with constant 45% SM and by 12.86% when comparing with 5–30% SM levels ($p < 0.05$) (Figs. 2c and 3b). Moreover, at the order level, the relative abundance of *Sordariales* was 17.82% in the constant 30% SM, which was significantly higher than those under other SM levels ($p < 0.05$). The relative abundances of *Hypocreales*, *Mortierellales* and *Eurotiales* were increased after wetting procedure of 5–30% and those of *Pleosporales* and *Agaricales* were decreased ($p < 0.05$) compared with situation under the constant 30% SM. Similarly, the relative abundance of *Mortierellales* was increased after the wetting procedure of 5–30–45% and those of *Pleosporales, Helotiales* and *Eurotiales* were decreased compared with situation under the constant 45% SM ($p < 0.05$) (Figs. 2d and 4b).

3.3. Comparison of bacterial and fungal co-occurrence network

The bacterial and fungal networks showed different co-occurrence patterns, typically with greater numbers of edges in the bacterial networks. There were more positive than negative correlations in both the bacteria and fungi networks. The bacterial average degree and

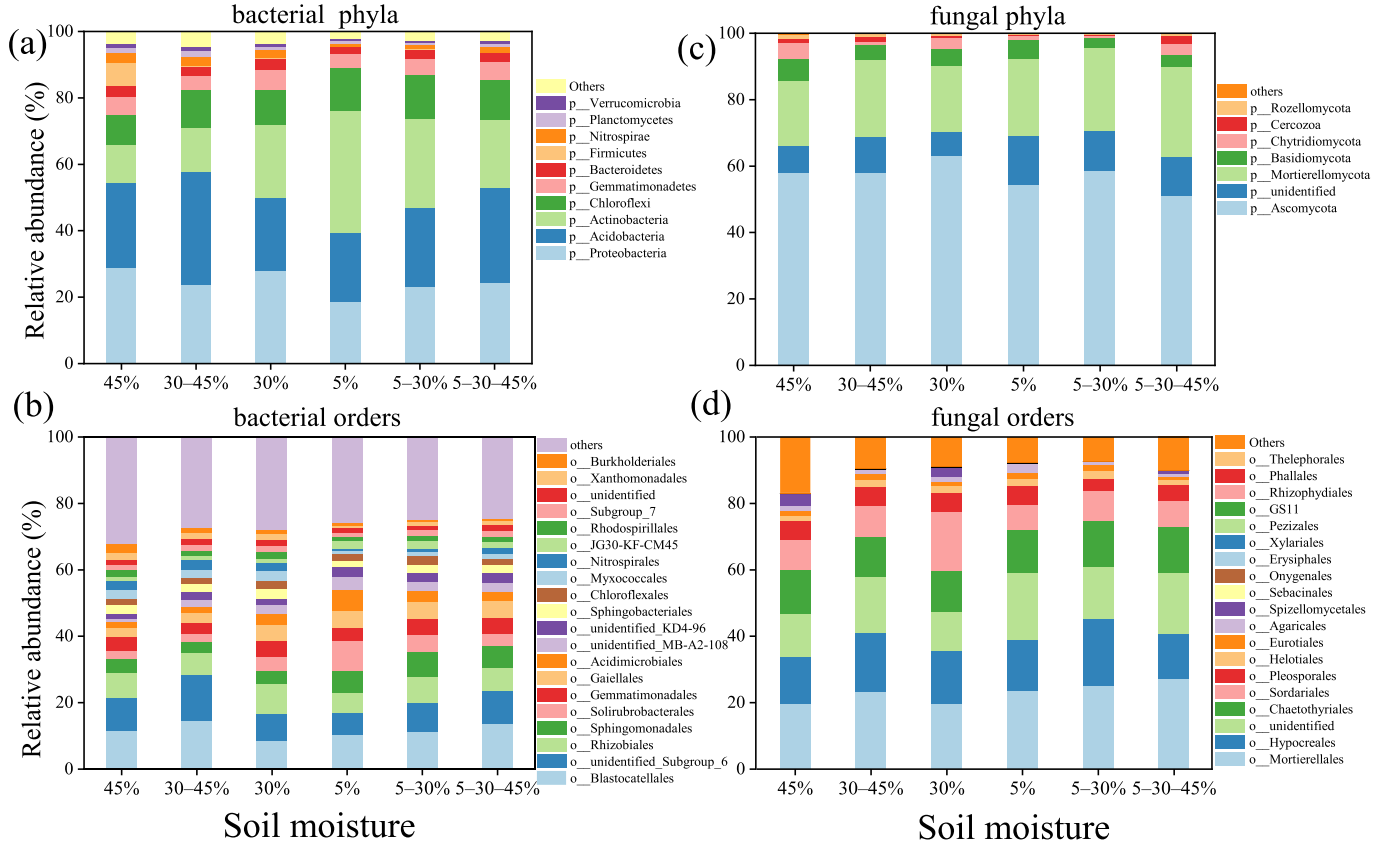


Fig. 2. Relative abundance of bacterial (a) (b) and fungal (c) (d) communities at the phylum (a) (c) and order (b) (d) levels across different SM levels. The values of 45%, 30% and 5% represent the SM being held constant at 45%, 30% and 5% levels, respectively; 5–30% represents the wetting procedure with SM being increased from 5% to 30%, with the same explanations for 5–30–45% and 30–45%.

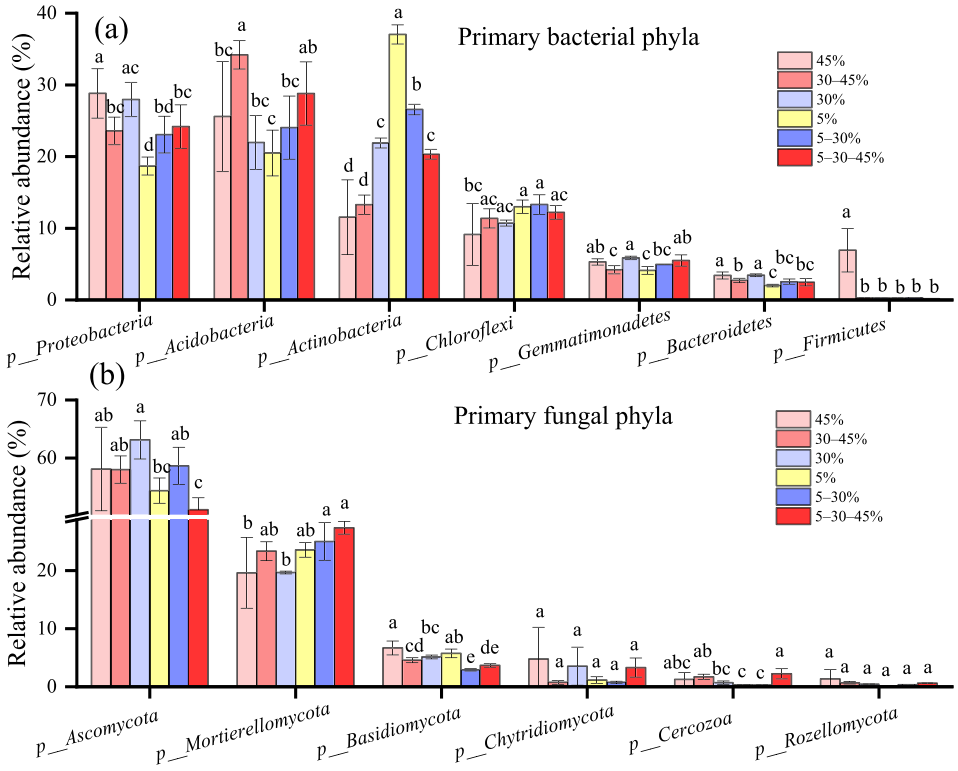


Fig. 3. Comparison of the relative abundances of dominant bacterial (a) and fungal (b) taxa at the phylum level under different SM levels. The values of 45%, 30% and 5% represent the SM being held constant at 45%, 30% and 5% levels, respectively; 5–30% represents the wetting procedure with SM being increased from 5% to 30%, with the same explanations for 5–30–45% and 30–45%. Plots labeled with the same letter are not significantly different at the $p < 0.05$ level.

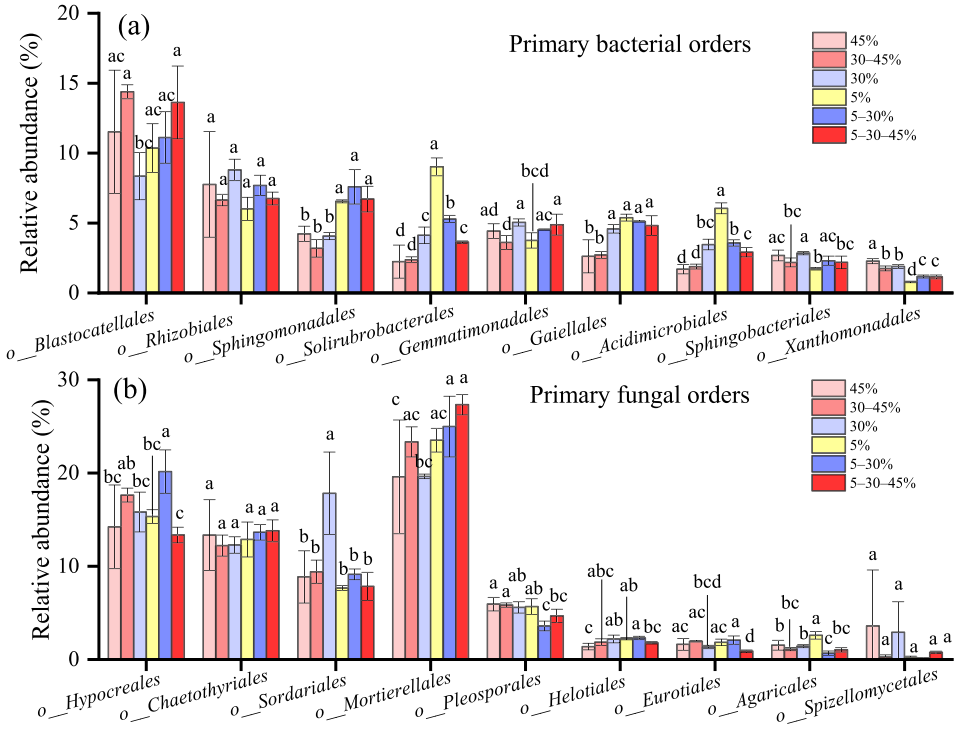


Fig. 4. Comparison of the relative abundances of dominant bacterial (a) and fungal (b) taxa at the order level under different SM levels. The values of 45%, 30% and 5% represent the SM being held constant at 45%, 30% and 5% levels, respectively; 5–30% represents the wetting procedure with SM being increased from 5% to 30%, with the same explanations for 5–30–45% and 30–45%. Plots labeled with the same letter are not significantly different at the $p < 0.05$ level.

average weighted degree were 16.40 and 7.56, respectively, which were much higher than those of the fungi at 3.33 and 0.99, respectively. The values of the average clustering coefficient and modularity in the bacterial networks were higher than those in the fungal networks, whereas average path length followed the opposite trend, suggesting that the bacteria had a prominent 'small-world' modularity and hierarchy of topological properties (Table S2). In particular, the dominant *Actinobacteria*, *Acidobacteria* and *Proteobacteria* showed highly positive correlations with other bacteria, and *Ascomycota* presented strong positive correlations with other fungi in different SM levels. The modularity in bacterial and fungal networks was all greater than 0.4, indicating that the networks of bacteria and fungi were modular (Fig. 5a and b).

3.4. Changes in soil microbial respiration rate

Declining trends were observed for the microbial respiration rate in the constant 30% and 45% SM (Fig. 6a). When the constant SM was increased from 5% to 45%, microbial respiration increased slightly. The respiration rates in the constant 5% SM condition slightly decreased across all incubation times. During the wetting procedure of 5–30–45%, the respiration rate significantly increased from 0.04 μg CO_2-C/g soil/day in the SM level of 5% at 16 days to 1.18 μg CO_2-C/g soil/day at 17 days and 4.81 μg CO_2-C/g soil/day at 23 days after wetting to a SM level of 30%, before peaking at 7.96 μg CO_2-C/g soil/day at 24 days after further increasing the SM level to 45%, which was 119.28% higher than the respiration rate of 3.63 μg CO_2-C/g soil/day in the wetting procedure of 30–45% at 24 days. The respiration rate in wetting procedure of 5–30% increased from 0.13 μg CO_2-C/g soil/day at the 23 days to 0.61 μg CO_2-C/g soil/day at the 24 days and further increased to 3.44 μg CO_2-C/g soil/day on the 27 days, which were lower than those in the wetting procedure of 5–30–45% at the days of 16–27 (Fig. 6).

The multiple stepwise linear regression results (Table S3) show that the soil microbial respiration rate was substantially influenced by bacterial richness (Chao 1) for the constant 45% SM level and the wetting procedures of 5–30–45% and 30–45%, with this richness explaining up to 84.40% of the variance ($p < 0.05$). The respiration rate was also influenced by bacterial Shannon diversity between the constant SM level of 30% and the wetting procedure of 5–30%, with explained variability of up to 94.90% and bacterial Shannon diversity and fungal beta diversity (PCAs) among the constant SM levels of 5%, 30% and 45%, with explained variability of 89.50% ($p < 0.05$).

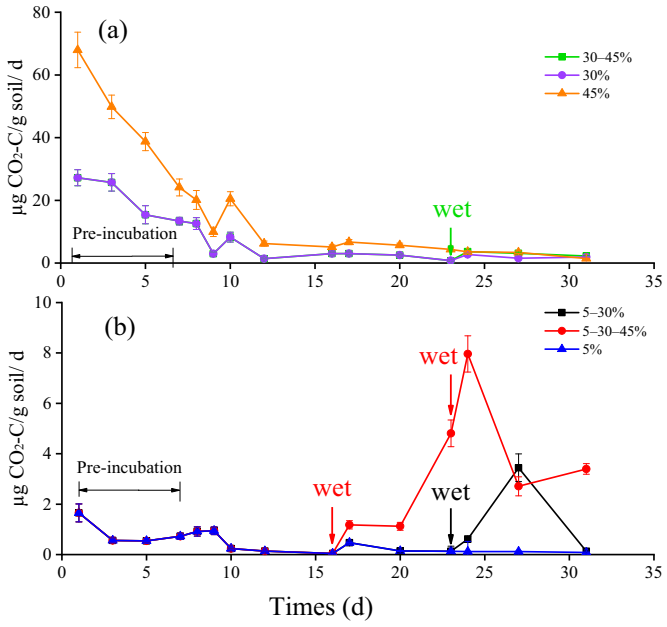


Fig. 6. C mineralization rate for the different SM levels. The vertical bars represent the standard errors of the mean.

4. Discussion

4.1. Soil microbial richness and diversity induced by the different moisture levels

Generally, distinct richness and diversity were observed for bacteria under different SM conditions, whereas fungal response to SM changing exhibited no obvious difference, indicating bacteria were more sensitive to the changing of SM than those of fungi. The PCAs results also revealing that bacterial communities demonstrated stronger clustering than fungal communities under different moisture conditions.

Bacterial richness was dramatically increased with an increase in SM from 5% to 30% and significantly higher than initially constant SM of 5%; however, the richness at the target moisture condition of 30% was still lower than that with SM being kept constant at 30%, revealing that the wetting history from low to medium SM produced a negative effect

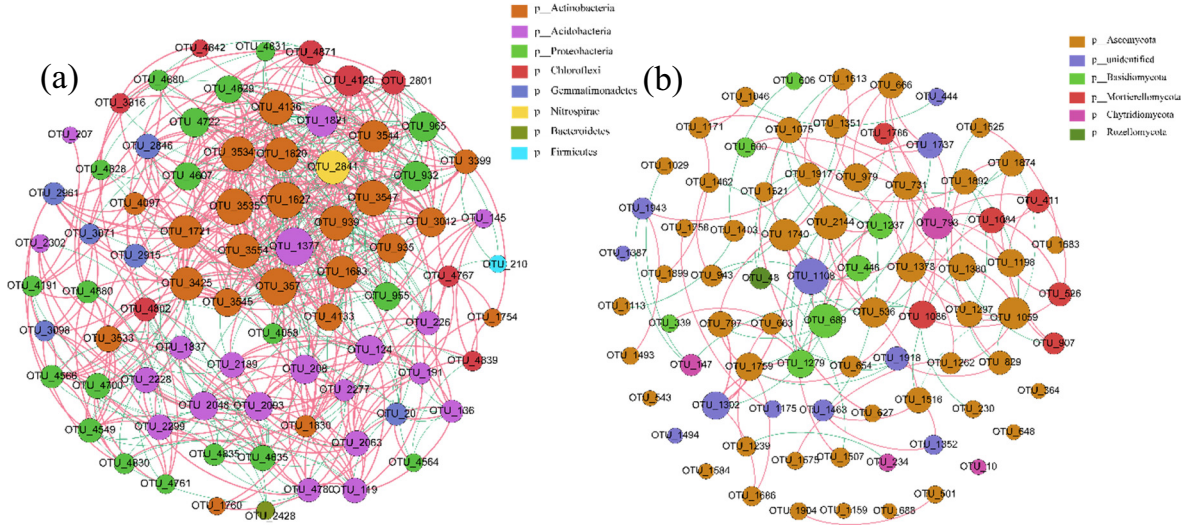


Fig. 5. Co-occurrence network of bacteria (a) and fungi (b) under different SM conditions. Each node represents individual OTUs, an edge represents a Spearman correlation with a correlation coefficient of >0.6, a red edge indicates a positive interaction, and a green edge indicates a negative interaction.

on bacterial richness. The observed hysteresis of the growth in bacterial richness with the wetting process may result from the adaptation of bacterial community to the wetting circumstance, which was in good agreement with the results of other studies (Bouskill et al., 2013; Preece et al., 2019). Furthermore, bacterial diversity in the constant 5% SM condition was significantly lower than those in the constant 30% SM conditions, possibly due to the delay in recovery of bacterial activity in the low SM condition (Nguyen et al., 2018). However, both of bacterial richness and diversity in constant 45% SM were slightly lower than those in constant 30% SM and those in the wetting procedure to 45% (i.e. 5–30–45% and 30–45%). The results indicated that excessive moisture to high SM did not contribute to, or even inhibit, the further enhancement of bacterial richness and diversity (McHugh and Schwartz, 2016).

In contrast to the bacteria, fungal richness and diversity exhibited no significant change with variation of the SM. This may be due to the fact that fungal hyphae facilitate access to water (Orwin et al., 2016), and their chitinous cell walls enhance their resistance to SM changes (Preece et al., 2019). Moreover, the changes of diversity in bacterial and fungi were lesser than richness, indicating variation of SM may disturb the ecological function of soil microbial communities, instead of the stability of soil ecosystems (Na et al., 2019).

4.2. Soil microbial community composition and network induced by the different moisture levels

As for the dominant bacterial species at the phylum level, both *Proteobacteria* and *Firmicutes* preferred high wet conditions (>30%); however, *Firmicutes* adapted slowly to changes in the SM condition. As gram-negative bacteria, *Proteobacteria* are much more resilient with the increase of SM (Banerjee et al., 2016), vulnerable to the water limitation (Nguyen et al., 2018), whereas they are also previously identified as positive responded to moisture (Placella et al., 2012; McHugh et al., 2014). The relative abundance of *Firmicutes* was only highest in the constant 45% SM with no obvious variation under other different SM conditions. Furthermore, *Firmicutes* was less resilient than *Proteobacteria*, which is attributable to the *Proteobacteria* phylum's being characterized as fast-growth copiotrophs when under suitable conditions (Liu et al., 2020). It is interesting to note that *Acidobacteria* adapted well to a range of different SM levels, which is consistent with the results of other studies that have reported *Acidobacteria* as being diverse and highly abundant in many physiologically and ecologically different environments (Barns et al., 1999; Singh et al., 2007). Moreover, the wetting process initially from 5% or 30%, especially 30%, significantly stimulate the abundance of *Acidobacteria*, presenting a pattern of adaptation to wet condition similar to that of *Proteobacteria*, which likely can be attributed to their similar ecological niches and close relationships at both the phylogenetic (Smit et al., 2001) and protein (Quaiser et al., 2003) levels from the physiological perspectives. However, the relative abundance of *Actinobacteria* was highest at the SM level of 5%, decreasing significantly during the wetting procedures of 5–30–45% and 5–30%. After the wetting processes were completed, the abundance of *Actinobacteria* was remarkably higher than that at the corresponding constant 45% and 30% SM, respectively. Therefore, *Actinobacteria* was prevalent in dry soils, which is supported by the reported increase of relative abundance of *Actinobacteria* in drought conditions (Barnard et al., 2013; Preece et al., 2019) and long-lasting effects on soil bacterial communities in low SM conditions (de Vries et al., 2018). These findings may be explained by *Actinobacteria*'s gram-positive nature, which includes the capability of forming spores to ensure survival and entering a dormant state in which metabolic activity becomes very low under environmental stress, especially during drought conditions. The increased relative abundance of *Actinobacteria* in drying period may be due to the preparation for next nutrient acquisition (Zhou et al., 2016). Similar results have been obtained in different ecosystems, including grasslands, forests, and arable land (Uhlířová et al., 2005; Swallow and Quideau, 2013; de Vries et al., 2018; Nguyen et al., 2018). Similar to *Actinobacteria*, *Chloroflexi* were also resistant to low SM and adapted well under different SM levels, which were consistent with results of previous studies (Lee et al., 2018; Nguyen et al., 2018). Conversely, the abundances of *Gemmatimonadetes* and *Bacteroidetes* were clearly inhibited at the 5% SM level, due to their gram-negative properties and susceptibility to environmental disturbance and water limitation (Schimel et al., 2007). Increased SM was beneficial to the transportation of organic matter to *Gemmatimonadetes* and *Bacteroidetes* and their growth (Na et al., 2019).

Unlike bacteria that exhibited obvious differences in relative abundance across all wetting procedures of 5–30%, 5–30–45% and 30–45% and constant SM levels of 5%, 30% and 45%, obvious difference was only detected for fungi when comparing the wetting process of 5–30–45% and constant SM of 45%. The relative abundance of *Ascomycota* increased as constant SM increased from 5% to 30% and decreased as the constant SM further increased to 45%. Similarly, the growth of *Ascomycota* was promoted when SM was below 30% and inhibited when SM was increased to 45% during the wetting process of 5–30–45%. The increased SM benefited the abundance of *Ascomycota*, while the excessive moisture posed the negative effect, which was consistent with trend for the relative abundance of *Pleosporales*, *Helotiales* and *Eurotiales* with the increase of SM at the order level (Bastida et al., 2017). The relative abundance of *Basidiomycota* exhibited opposite pattern to be high in the 5% SM (Bastida et al., 2017).The results indicate that the fungi were more tolerant to water stress than the bacteria. This seems to support our first hypothesis: that soil bacterial activity would be more sensitive to changes in the SM condition than fungi and that the bacterial communities would be less resistant than fungi, especially in some extreme conditions. This phenomenon could be explained by the characteristic of fungi accessing nutrient through hyphal networks and the rapid turnover of populations conferring high plasticity to the fungal communities (Kaisermann et al., 2015). The SM influenced the fungi through rapid germination, sporulation and the development of mycelial cord (McLean and Huhta, 2000). The low SM condition was likely to facilitate survival of fungi due to the filamentous nature preferring to aerobic conditions improved by drought (Ma et al., 2015), however, fungi may be destabilized in the high SM condition (Canarini et al., 2017).

The differences between the bacterial and fungal communities were also verified through network analysis. Under variation of the SM, the soil fungal communities with less diversity and richness exhibited a less-linked network structure, however, the most dominant bacterial taxa showed strongest response to the variation of SM (more edges, higher average degree and average weighted degree), revealing that bacteria is more sensitive to the variation of SM than fungi (de Vries et al., 2018; Yang et al., 2020). In short, bacterial diversity, richness and interaction are more highly sensitive to different levels of SM than fungi.

4.3. Soil microbial respiration rate under different moisture levels

Respiration rate was decreased across the entirety of incubation, two or one step of continual wetting causing the pulse of CO_2 fluxes. Moreover, the size of pluses after the second wetting declined over the incubation time. This may be attributable to the limitation of labile substrates and oxygen as well as the accumulation of CO_2 during incubation (Orchard and Cook, 1983). In the constant low SM (5%), the movement of organic carbon could become "torpid" in the "chemically sticky" soil environment, resulting in decreased microbial activity and lower respiration rate accompanying the incubation (Xiang et al., 2008). Generally, fungi are thought to be more tolerant than bacteria to the drying condition. The fungi maintained high respiration rate during the drying period, which was attributed to their capacity to accumulate osmoregulatory solutes that do not impair metabolism and to their filamentous structure, reaching and exploiting substrates even at very low SM levels by bridging the air-filled pores with low diffusivity using hyphal (Orchard and Cook, 1983; Manzoni et al., 2012).

Additionally, the respiration rate of bacteria increased after the second rewetting. Upon rewetting of dry soil, available substrates were mobilized, stimulating the growth of microbes, especially bacteria, resulting in the pulse of CO_2 emissions. This could be explained by the increasing of substrates attributed to the dissolved organic carbon (DOC) from dead soil microbes or other biomass in the drying period (Kieft et al., 1987; Butterly et al., 2010; Xiao et al., 2017; Lu et al., 2020). When the soils were rewetted and SM increased, the soil water potential was decreased according to the soil-water characteristic curve of the soil used in the study (Fig. S2). As a consequent, equivalent pore diameter of soil was increased and some organic materials would be desorbed from soil particles, rearranging into the dissolved phase (Blagodatsky and Smith, 2012), which would be conducive to microbial intake and the abrupt improvement of respiration. The surviving microbes in the drying period would contribute to the increased CO_2 emissions by their rapid growth rate under the more beneficial environmental variation during the wetting procedure (Xiang et al., 2008). However, further rewetting process may result in the destabilization of fungi more than bacteria, and consequently bacteria could maintain high respiration rate in the wetting period (Canarini et al., 2017).

At the later incubation time during the wetting procedure of 5–30%, the pulse of CO_2 emission was much lower than expected after wetting, which cannot be explained by easy consumption of the substrate accumulated in the earlier dry stage. This phenomenal may also be the result of the activation of different bacteria and fungi and limitation of oxygen (Preece et al., 2019; Zhu et al., 2020). Wetting process of 5–30% in the later stage stimulated the microbial groups with preference to wet condition, including bacteria groups of *Acidobacteria*, *Proteobacteria*, *Gemmatimonadetes* and *Bacteroidetes* and fungi group of *Ascomycota*. However, this stimulation on bacteria and fungi is not immediate after the long time under low previous SM condition (Meisner et al., 2015; Meisner et al., 2017). Meanwhile, the similar decline in respiration rate at the later incubation stage in the constant 45% and 30% SM and the wetting procedure of 30–45% may be due to the same reason as well as the concentrating of CO_2 along with the incubation. This may lead to the different community composition in different SM levels. Compared the wetting procedure of 5–30% or 30–45% with 5–30–45%, the different respiration rate after increasing SM to the same value (i.e. 30% or 45%), may be attributed to the deliberately delayed time of increasing SM in the wetting procedure of 5–30% or 30–45%, which was one limitation of experimental procedure in the study. Therefore, the second hypothesis about the existence of respiration rate pulses in the two gradual wetting procedures was verified and the first hypothesis about the different respiration rate between bacteria and fungi was explained. Bacterial and fungal diversity were verified as the primary explanatory factors for microbial respiration rate under different SM conditions.

5. Conclusion

The wetting procedure led to differences between bacterial and fungal communities and respiration rates in the eroded soil obtained from the natural vegetation area on the Loess Plateau. Bacterial diversity and richness were positively correlated to the SM levels, and the bacterial communities were more sensitive than fungi in the wetting procedure. In particular, *Proteobacteria* and *Firmicutes* preferred wet conditions, and the phylum of *Proteobacteria* was more resilient than *Firmicutes*. *Actinobacteria* prevailed in dry condition, and its relative abundance was influenced largely by the wetting history of its soil. *Acidobacteria*, similar to *Proteobacteria*, was highly abundant in high SM. The dominant bacterial communities converted from *Actinobacterial* to *Proteobacteria* and *Acidobacteria* as SM increased from 5% to 45%. However, no differences for the *Chloroflexi* communities were observed across any sample. The relative abundance of *Ascomycota* increased as SM increased from 5% to 30% and decreased as SM further increased to 45%. Additionally, the gradual wetting procedure would cause a slight respiration pulse, while an overall downward trend was observed in respiration rate as incubation progressed. Our results provided essential information by which to estimate the responses of soil microbial composition, the phylum-levels network and respiration behavior to changes in SM and by which to assess the effect of intense wetting events on microbial stability and the carbon cycle for better management of plant-soil-water relationship in the ecosystem after natural vegetation restoration on the Loess Plateau.

CRediT authorship contribution statement

Panpan Jiao: Conceptualization, Methodology, Writing - original draft, Visualization. **Zhongwu Li:** Methodology, Validation, Writing - review & editing. **Lei Yang:** Visualization, Methodology, Writing - review & editing. **Jijun He:** Writing - review & editing. **Xiaofeng Chang:** Formal analysis. **Haibing Xiao:** Resources. **Xiaodong Nie:** Supervision. **Di Tong:** Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was financially supported by the 'Hundred-talent Project' of the Chinese Academy of Sciences (A315021407).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.143899.

References

Banerjee, S., Helgason, B., Wang, L., Winsley, T., Ferrari, B.C., Siciliano, S.D., 2016. Legacy effects of soil moisture on microbial community structure and N_2O emissions. Soil Biol. Biochem. 95, 40–50.

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

Barns, S.M., Takala, S.L., Kuske, C.R., 1999. Wide distribution and diversity of members of the bacterial kingdom Acidobacterium in the environment. Appl. Environ. Microbiol. 65, 1731.

Bastida, F., Torres, I.F., Andres-Abellan, M., Baldrian, P., Lopez-Mondejar, R., Vetrovsky, T., Richnow, H.H., Starke, R., Ondono, S., Garcia, C., Lopez-Serrano, F.R., Jehmlich, N., 2017. Differential sensitivity of total and active soil microbial communities to drought and forest management. Glob. Chang. Biol. 23, 4185–4203.

Birch, H.F., 1959. Further observations on humus decomposition and nitrification. Plant Soil 11, 262–286.

Blagodatsky, S., Smith, P., 2012. Soil physics meets soil biology: towards better mechanistic prediction of greenhouse gas emissions from soil. Soil Biol. Biochem. 47, 78–92.

Bouskill, N.J., Lim, H.C., Borglin, S., Salve, R., Wood, T.E., Silver, W.L., Brodie, E.L., 2013. Pre-exposure to drought increases the resistance of tropical forest soil bacterial communities to extended drought. ISME J. 7, 384–394.

Butterly, C., Marschner, P., McNeill, A., Baldock, J., 2010. Rewetting CO_2 pulses in Australian agricultural soils and the influence of soil properties. Biol. Fertil. Soils 46, 739–753.

Canarini, A., Kiær, L.P., Dijkstra, F.A., 2017. Soil carbon loss regulated by drought intensity and available substrate: a meta-analysis. Soil Biol. Biochem. 112, 90–99.

Carson, J.K., Gonzalez-Quiñones, V., Murphy, D.V., Hinz, C., Shaw, J.A., Gleeson, D.B., 2010. Low pore connectivity increases bacterial diversity in soil. Appl. Environ. Microbiol. 76, 3936.

Das, S., Richards, B.K., Hanley, K.L., Krounbi, L., Walter, M.F., Walter, M.T., Steenhuis, T.S., Lehmann, J., 2019. Lower mineralizability of soil carbon with higher legacy soil moisture. Soil Biol. Biochem. 130, 94–104.

de Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Girlanda, M., Gweon, H.S., Hallin, S., Kaisermann, A., Keith, A.M., Kretzschmar, M., Lemanceau, P., Lumini, E., Mason, K.E., Oliver, A., Ostle, N., Prosser, J.I., Thion, C., Thomson, B., Bardgett, R.D., 2018. Soil bacterial networks are less stable under drought than fungal networks. Nat. Commun. 9, 3033.

Deng, Q., Cheng, X., Hui, D., Zhang, Q., Li, M., Zhang, Q., 2016. Soil microbial community and its interaction with soil carbon and nitrogen dynamics following afforestation in central China. Sci. Total Environ. 541, 230–237.

Duan, X., Liu, B., Gu, Z., Rong, L., Feng, D., 2016. Quantifying soil erosion effects on soil productivity in the dry-hot valley, southwestern China. Environ. Earth Sci. 75, 1164.
Evans, S.E., Wallenstein, M.D., 2012. Soil microbial community response to drying and rewetting stress: does historical precipitation regime matter? Biogeochemistry 109, 101–116.
Fierer, N., Schimel, J.P., Holden, P.A., 2003. Influence of drying–rewetting frequency on soil bacterial community structure. Microb. Ecol. 45, 63–71.
Fu, X., Shao, M., Wei, X., Wang, H., Zeng, C., 2013. Effects of monovegetation restoration types on soil water distribution and balance on a hillslope in northern Loess Plateau of China. J. Hydrol. Eng. 18, 413–421.
Gao, X., Li, W., Salman, A., Wang, R., Du, L., Yao, L., Hu, Y., Guo, S., 2020. Impact of topsoil removal on soil CO_2 emission and temperature sensitivity in Chinese Loess Plateau. Sci. Total Environ. 708, 135102.
Griffiths, R.I., Whiteley, A.S., O'Donnell, A.G., Bailey, M.J., 2003. Physiological and community responses of established grassland bacterial populations to water stress. Appl. Environ. Microbiol. 69, 6961–6968.
Hawkes, C.V., Waring, B.G., Rocca, J.D., Kivlin, S.N., 2017. Historical climate controls soil respiration responses to current soil moisture. Proc. Natl. Acad. Sci. 114, 6322.
He, D., Shen, W., Eberwein, J., Zhao, Q., Ren, L., Wu, Q.L., 2017. Diversity and co-occurrence network of soil fungi are more responsive than those of bacteria to shifts in precipitation seasonality in a subtropical forest. Soil Biol. Biochem. 115, 499–510.
Kaisermann, A., Maron, P.A., Beaumelle, L., Lata, J.C., 2015. Fungal communities are more sensitive indicators to non-extreme soil moisture variations than bacterial communities. Appl. Soil Ecol. 86, 158–164.
Kalembasa, S.J., Jenkinson, D.S., 1973. A comparative study of titrimetric and gravimetric methods for the determination of organic carbon in soil. J. Sci. Food Agric. 24, 1085–1090.
Kieft, T.L., Soroker, E., firestone, M.K., 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biol. Biochem. 19, 119–126.
Kim, D.G., Vargas, R., Bond-Lamberty, B., Turetsky, M., 2012. Effects of soil rewetting and thawing on soil gas fluxes: a review of current literature and suggestions for future research. Biogeosciences 9, 2459–2483.
Kjeldahl, J., 1883. Neue Methode zur Bestimmung des Stickstoffs in organischen Körpern. Z. Anal. Chem. 22, 366–382.
Lee, K.C., Caruso, T., Archer, S.D.J., Gillman, L.N., Lau, M.C.Y., Cary, S.C., Lee, C.K., Pointing, S.B., 2018. Stochastic and deterministic effects of a moisture gradient on soil microbial communities in the McMurdo Dry Valleys of Antarctica. Front. Microbiol. 9.
Liu, C., Li, L., Xie, J., Coulter, J.A., Zhang, R., Luo, Z., Cai, L., Wang, L., Gopalakrishnan, S., 2020. Soil bacterial diversity and potential functions are regulated by long-term conservation tillage and straw mulching. Microorganisms 8.
Lu, T., Wang, Y., Zhu, H., Wei, X., Shao, M., 2020. Drying-wetting cycles consistently increase net nitrogen mineralization in 25 agricultural soils across intensity and number of drying-wetting cycles. Sci. Total Environ. 710, 135574.
Ma, L., Guo, C., Lü, X., Yuan, S., Wang, R., 2015. Soil moisture and land use are major determinants of soil microbial community composition and biomass at a regional scale in northeastern China. Biogeosciences 12, 2585–2596.
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., 2016. A watering manipulation in a semiarid grassland induced changes in fungal but not bacterial community composition. Pedobiologia 59, 121–127.
McHugh, T.A., Koch, G.W., Schwartz, E., 2014. Minor changes in soil bacterial and fungal community composition occur in response to monsoon precipitation in a semiarid grassland. Microb. Ecol. 68, 370–378.
McLean, M.A., Huhta, V., 2000. Temporal and spatial fluctuations in moisture affect humus microfungal community structure in microcosms. Biol. Fertil. Soils 32, 114–119.
Meisner, A., Rousk, J., Bååth, E., 2015. Prolonged drought changes the bacterial growth response to rewetting. Soil Biol. Biochem. 88, 314–322.
Meisner, A., Leizeaga, A., Rousk, J., Bååth, E., 2017. Partial drying accelerates bacterial growth recovery to rewetting. Soil Biol. Biochem. 112, 269–276.
Na, X., Yu, H., Wang, P., Zhu, W., Niu, Y., Huang, J., 2019. Vegetation biomass and soil moisture coregulate bacterial community succession under altered precipitation regimes in a desert steppe in northwestern China. Soil Biol. Biochem. 136, 107520.
Nguyen, L.T.T., Osanai, Y., Lai, K., Anderson, I.C., Bange, M.P., Tissue, D.T., Singh, B.K., 2018. Responses of the soil microbial community to nitrogen fertilizer regimes and historical exposure to extreme weather events: flooding or prolonged-drought. Soil Biol. Biochem. 118, 227–236.
Nie, X., Li, Z., Huang, J., Liu, L., Xiao, H., Liu, C., Zeng, G., 2018. Thermal stability of organic carbon in soil aggregates as affected by soil erosion and deposition. Soil Tillage Res. 175, 82–90.
Orchard, V.A., Cook, F.J., 1983. Relationship between soil respiration and soil moisture. Soil Biol. Biochem. 15, 447–453.
Orgiazzi, A., Panagos, P., 2018. Soil biodiversity and soil erosion: it is time to get married. Glob. Ecol. Biogeogr. 27, 1155–1167.
Orwin, K.H., Dickie, I.A., Wood, J.R., Bonner, K.I., Holdaway, R.J., 2016. Soil microbial community structure explains the resistance of respiration to a dry–rewet cycle, but not soil functioning under static conditions. Funct. Ecol. 30, 1430–1439.
Pesaro, M., Nicollier, G., Zeyer, J., Widmer, F., 2004. Impact of soil drying-rewetting stress on microbial communities and activities and on degradation of two crop protection products. Appl. Environ. Microbiol. 70, 2577.
Piao, S., Ciais, P., Huang, Y., Shen, Z., Peng, S., Li, J., Zhou, L., Liu, H., Ma, Y., Ding, Y., Friedlingstein, P., Liu, C., Tan, K., Yu, Y., Zhang, T., Fang, J., 2010. The impacts of climate change on water resources and agriculture in China. Nature 467, 43–51.
Placella, S.A., Brodie, E.L., Firestone, M.K., 2012. Rainfall-induced carbon dioxide pulses result from sequential resuscitation of phylogenetically clustered microbial groups. Proc. Natl. Acad. Sci. 109, 10931.
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 Biol. Biochem. 131, 28–39.
Quaiser, A., Ochsenreiter, T., Lanz, C., Schuster, S.C., Treusch, A.H., Eck, J., Schleper, C., 2003. Acidobacteria form a coherent but highly diverse group within the bacterial domain: evidence from environmental genomics. Mol. Microbiol. 50, 563–575.
Ren, C., Sun, P., Kang, D., Zhao, F., Feng, Y., Ren, G., Han, X., Yang, G., 2016. Responsiveness of soil nitrogen fractions and bacterial communities to afforestation in the Loess Hilly Region (LHR) of China. Sci. Rep. 6, 28469.
Ren, C., Zhao, F., Shi, Z., Chen, J., Han, X., Yang, G., Feng, Y., Ren, G., 2017. Differential responses of soil microbial biomass and carbon-degrading enzyme activities to altered precipitation. Soil Biol. Biochem. 115, 1–10.
Ren, C., Wang, T., Xu, Y., Deng, J., Zhao, F., Yang, G., Han, X., Feng, Y., Ren, G., 2018. Differential soil microbial community responses to the linkage of soil organic carbon fractions with respiration across land-use changes. For. Ecol. Manag. 409, 170–178.
Schimel, J., Balser, T.C., Wallenstein, M., 2007. Microbial stress-response physiology and its implications for ecosystem function. Ecology 88, 1386–1394.
Singh, B.K., Munro, S., Potts, J.M., Millard, P., 2007. Influence of grass species and soil type on rhizosphere microbial community structure in grassland soils. Appl. Soil Ecol. 36, 147–155.
Smit, E., Leeflang, P., Gommans, S., van den Broek, J., van Mil, S., Wernars, K., 2001. Diversity and seasonal fluctuations of the dominant members of the bacterial soil community in a wheat field as determined by cultivation and molecular methods. Appl. Environ. Microbiol. 67, 2284.
Swallow, M., Quideau, S.A., 2013. Moisture effects on microbial communities in boreal forest floors are stand-dependent. Appl. Soil Ecol. 63, 120–126.
Tong, D., Xiao, H., Li, Z., Nie, X., Huang, J., 2020. Stand ages adjust fluctuating patterns of soil respiration and decrease temperature sensitivity after revegetation. Soil Sci. Soc. Am. J. 84, 760–774.
Uhlířová, E., Elhottová, D., Tříska, J., Šantrůčková, H., 2005. Physiology and microbial community structure in soil at extreme water content. Folia Microbiol. 50, 161.
Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707.
Vivoni, E.R., Rinehart, A.J., Méndez-Barroso, L.A., Aragón, C.A., Bisht, G., Cardenas, M.B., Engle, E., Forman, B.A., Frisbee, M.D., Gutiérrez-Jurado, H.A., Hong, S.-h., Mahmood, T.H., Tai, K., Wyckoff, R.L., 2008. Vegetation controls on soil moisture distribution in the Valles Caldera, New Mexico, during the North American monsoon. Ecohydrology 1, 225–238.
Wang, X., Xiao, S., Yang, X., Liu, Z., Zhou, X., Du, G., Zhang, L., Guo, A., Chen, S., Nielsen, U.N., 2019. Dominant plant species influence nematode richness by moderating understory diversity and microbial assemblages. Soil Biol. Biochem. 137, 107566.
Xiang, S.-R., Doyle, A., Holden, P.A., Schimel, J.P., 2008. Drying and rewetting effects on C and N mineralization and microbial activity in surface and subsurface California grassland soils. Soil Biol. Biochem. 40, 2281–2289.
Xiao, L., Liu, G., Zhang, J., Xue, S., 2016. Long-term effects of vegetational restoration on soil microbial communities on the Loess Plateau of China. Restor. Ecol. 24, 794–804.
Xiao, H., Li, Z., Dong, Y., Chang, X., Deng, L., Huang, J., Nie, X., Liu, C., Liu, L., Wang, D., Liu, Q., Zhang, Y., 2017. Changes in microbial communities and respiration following the revegetation of eroded soil. Agric. Ecosyst. Environ. 246, 30–37.
Xu, H., Wang, X., Qu, Q., Zhai, J., Song, Y., Qiao, L., Liu, G., Xue, S., 2020. Cropland abandonment altered grassland ecosystem carbon storage and allocation and soil carbon stability in the Loess Hilly Region, China. Land Degrad. Dev. 31, 1001–1013.
Yang, Y., Cheng, H., Liu, L., Dou, Y., An, S., 2020. Comparison of soil microbial community between planted woodland and natural grass vegetation on the Loess Plateau. For. Ecol. Manag. 460, 117817.
Zhang, Y., Shangguan, Z., 2016. The coupling interaction of soil water and organic carbon storage in the long vegetation restoration on the Loess Plateau. Ecol. Eng. 91, 574–581.
Zhang, C., Liu, G., Xue, S., Wang, G., 2016. Soil bacterial community dynamics reflect changes in plant community and soil properties during the secondary succession of abandoned farmland in the Loess Plateau. Soil Biol. Biochem. 97, 40–49.
Zhou, X., Fornara, D., Ikenaga, M., Akagi, I., Zhang, R., Jia, Z., 2016. The resilience of microbial community under drying and rewetting cycles of three forest soils. Front. Microbiol. 7.
Zhu, Y.Z., Li, Y.Y., Zheng, N.G., Chapman, S.J., Yao, H.Y., 2020. Similar but not identical resuscitation trajectories of the soil microbial community based on either DNA or RNA after flooding. Agronomy-Basel 10, 21.