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Response of soil bacterial community and geochemical parameters to cyclic groundwater-level oscillations in laboratory columns

Xuefeng Xia[1,3,4] | **Lirong Cheng**[1,3,4] | **Yi Zhu**[1,3,4] | **Yueqiao Liu**[1,3,4] | **Kai Wang**[1,3,4] | **Aizhong Ding**[1,3,4] | **Zuansi Cai**[2] | **Huansheng Shi**[5] | **Lili Zuo**[5]

[1]College of Water Sciences, Beijing Normal Univ., Beijing 100875, China

[2]School of Engineering and the Built Environment, Edinburgh Napier Univ., Edinburgh EH10 5DT, UK

[3]Engineering Research Center of Groundwater Pollution Control and Remediation of Ministry of Education, Beijing Normal Univ., Beijing 100875, China

[4]Beijing Key Lab. of Urban Hydrological Cycle and Sponge City Technology, Beijing Normal Univ., Beijing, 100875 China

[5]China Railway Fifth Survey and Design Institute Group Company, Beijing 102600, China

Correspondence
Aizhong Ding, 12#, Xueyuannan Rd., Haidian District, 100875 Beijing, China.
Email: ading@bnu.edu.cn

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Abstract

Groundwater-level oscillations change geochemical conditions, C cycling processes, and bacterial community composition, and these changes may vary vertically with depth in a soil. In this study, soil column experiments were conducted to explore variations in soil bacterial community composition and its associated geochemical parameters to rapid short-term cyclic groundwater-level oscillations driven by natural fluctuations (NF) and rainfall infiltration (RI), and the results are compared with a quasistatic (QS) column. Water saturation patterns in vadose and oscillated zones, and O_2 level patterns, soil total organic C (TOC) removal rates, and soil bacterial community composition in vadose, oscillated, and saturated zones were evaluated. Results showed that water saturation and O_2 level oscillated with groundwater level in NF and RI columns. Total organic C removal rates in RI column were the highest across vadose (~38.4%), oscillated (~35.8%), and saturated (~35.2%) zones. Deltaproteobacteria, which were significantly correlated with TOC removal ($p < .05$), were found in higher abundance in the vadose and oscillated zones of the RI column than in the QS and NF columns. Soil bacterial community structure was dynamic at the class level due to water saturation, O_2 level, and TOC removal. Total organic C removal was the driver to separate the distribution of bacterial community structure in the vadose and oscillated zones of the RI column from those of the QS and NF columns. This study suggests that RI induced rapid, short-term, cyclic, groundwater-level oscillations could significantly influence both the soil C cycle and bacterial community structure in the vadose and oscillated zones.

1 | INTRODUCTION

Groundwater level usually oscillates due to hydrological dynamic factors such as natural fluctuations (NF), groundwater–surface water interactions (Krause, Bronstert, & Zehe, 2007), rainfall infiltration (RI) (Voisin, Cournoyer, Vienney, & Mermillod-Blondin, 2018), and anthropogenic factors like groundwater extracting and recharging.

Abbreviations: DOC, dissolved organic carbon; NF, natural fluctuations; NFC, natural fluctuation column; OTU, operational taxonomic unit; QS, quasistatic; QSC, quasistatic column; RDA, redundancy analysis; RI, rainfall infiltration; RIC, rainfall infiltration column; TOC, total organic carbon.

Groundwater-level oscillations lead to transport and redistribution of pollutants and soil components through interactions between soil and water (Almasri, 2007; Dai et al., 2019), and an alternating spatial–temporal distribution of soil moisture and O_2. These processes generate a depth profile in water saturation and the availability of electron donors and terminal electron acceptors (Farnsworth & Hering, 2011; Schimel, Balser, & Wallenstein, 2007; Zhou, Zhang, Dong, Lin, & Su, 2015), which in turn cause the soil bacterial community to develop different functional diversity at different depths (Pett-Ridge & Firestone, 2005). Soil bacterial communities can affect soil properties and quality through numerous important biogeochemical processes (Farnsworth, Voegelin, & Hering, 2012; Lipson et al., 2012; Meckenstock et al., 2015), eventually resulting in an impact on ecosystem functions (Huang et al., 2019). Therefore, it is important to investigate the response of soil bacterial community composition at different depths to groundwater-level-oscillation-induced geochemical conditions for better understanding the functions of soil ecosystems.

During groundwater-level oscillations, soil pore air may be replaced or entrapped and potentially dissolve into groundwater beneath groundwater level (Haberer, Rolle, Cirpka, & Grathwohl, 2012, 2014; Jost, Haberer, Grathwohl, Winter, & Gallert, 2015; Machler, Peter, Brennwald, & Kipfer, 2013), depending on the hydrodynamics of the specific imbibition pathway. Previous studies mostly focused on groundwater-level oscillations driven by NF, which is characterized by an upward flow of O_2–depleted groundwater that displaces soil pore air during increases in groundwater level, and an influx of pore air drawn in when groundwater level decrease, resulting in alternating reducing and oxidizing conditions in the oscillated zone (Yang et al., 2017). Less attention has been paid to groundwater-level oscillations driven by RI. In contrast, RI is characterized by downward flow of O_2–rich rainfall water that can entrap soil pore air in vadose and oscillated zones, potentially elevating O_2 level in the saturated zone (Neale, Hughes, & Ward, 2000; Van Driezum et al., 2018). Hence, O_2 level along with soil moisture content (or water saturation) will exhibit different temporal patterns within the vadose, oscillated, and saturated zones of an aquifer in response to NF and RI. As water and O_2 are key factors that drive biogeochemical processes (Borer, Tecon, & Or, 2018; Suenaga, Riya, Hosomi, & Terada, 2018), understanding the spatiotemporal distribution of water saturation and O_2 level in an aquifer is therefore a necessary first step to understanding the response of bacterial community composition at various depths to groundwater level variations. However, the effects of groundwater-level oscillations driven by these two different hydrological dynamic factors (NF and RI) on the spatiotemporal distribution of water saturation and O_2 level have rarely been reported (Davis, Laslett, Patterson, & Johnston, 2013).

Core Ideas

- Water saturation and O_2 level oscillated with groundwater level.
- Soil bacterial community structure was dynamic due to geochemical parameters.
- Rainfall infiltration could influence soil C cycle and bacterial communities.

Some researchers have reported that groundwater-level oscillations can change spatial distribution and transformation of pollutants (Dobson, Schroth, & Zeyer, 2007; Yang et al., 2017) and cause bacterial community composition shifts (Zhou et al., 2015) in contaminated aquifers. However, the effect of groundwater-level oscillations on bacterial community composition in natural aquifers is still less known. As soils in natural aquifers are abundant in organic C (Vos et al., 2019), the leaching, dissolution, and biodegradation of organic C can have an impact on the response of soil bacterial community composition at different depths over long-term, cyclic, groundwater-level oscillations (Rühle, von Netzer, Lueders, & Stumpp, 2015). It is possible that an impact on response of soil bacterial community composition at different depths can also occur in natural aquifers over rapid, short-term, cyclic, groundwater-level oscillations, as a previous study reported that short-term, groundwater-level oscillations can alter geochemical processes (Farnsworth et al., 2012). Moreover, rapid, short-term, cyclic, groundwater-level oscillations driven by NF and RI might cause different soil bacterial community composition responses. In order to understand the response of soil bacterial community composition at different depths to C cycle over rapid, short-term, cyclic, groundwater-level oscillations driven by NF and RI, it is necessary to explore removal rates of soil TOC at different depths and their corresponding bacterial community compositions.

Therefore, the objectives of this study were (a) to delineate the spatiotemporal distribution of water saturation and O_2 level, (b) to determine the removal rates of soil TOC, and (c) to characterize the bacterial community composition at different depths in quasistatic (QS) and two different rapidly oscillating aquifer scenarios (NF and RI). We tested the hypothesis that infiltration of O_2–rich rainfall water into aquifers due to RI can alter soil total organic C (TOC) removal rates and bacterial community structure in a more pronounced way than during NF (both are compared with a QS). We discuss the link of soil TOC removal, water saturation, and O_2 level related to bacterial community diversity and structure and provide insight into the impacts of rapid, short-term, cyclic, groundwater-level oscillations on the soil C cycle.

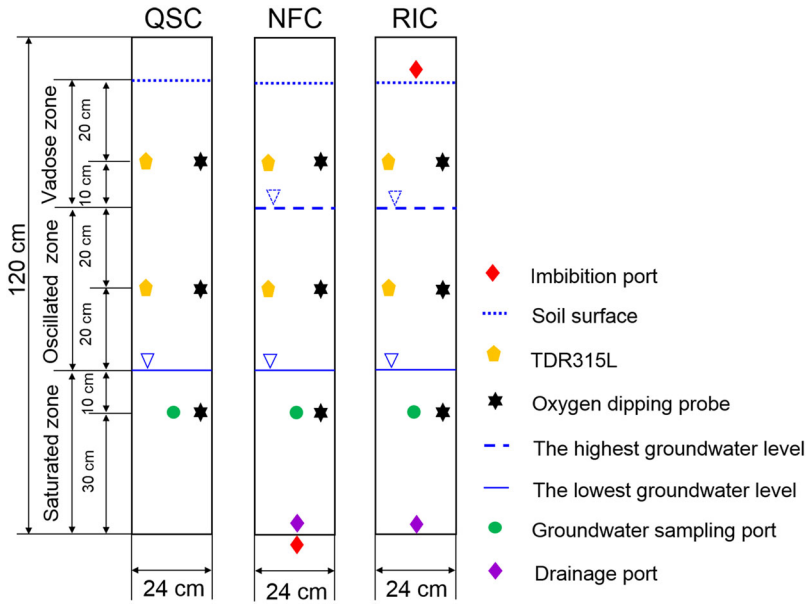

FIGURE 1 Schematic of the experimental system. The QSC represents the quasistatic column, NFC represents the natural fluctuation column, and RIC represents the rainfall infiltration column

2 | MATERIALS AND METHODS

2.1 | Soil column and groundwater-level oscillation regime

To study the effects of rapid, short-term, cyclic, groundwater-level oscillations on soil bacterial community and its associated geochemical parameters, three soil columns with a length of 120 cm and an internal diameter of 24 cm (Figure 1) were established to represent the QS (control) and two different hydrological dynamic conditions (NF and RI). The soil columns were filled with natural fine-grained river sand collected from Cihe (Shijiazhuang, China), and basic physical and chemical properties of the soil are summarized in Supplemental Table S1. The soils were packed into separate columns using a wet-packing procedure (i.e., the groundwater level was raised slowly to constantly maintain at a small depth of water above the top of soil surface to avoid entrapment of air, but also to minimize the separation of grain sizes due to different settling rates). Groundwater was mimicked by O_2–depleted tap water (prepared by stripping the necessary amount of tap water with N_2), and the physical and chemical properties of the groundwater are listed in Supplemental Table S2. The packed height was 110 cm, the compacted density was 1.60 g cm^{-3}, and the effective porosity was 0.35. The groundwater was fully drained after packing.

During the experiments, groundwater was injected from column bottom until the groundwater level reached a 40-cm height (Supplemental Table S2, 6,330 ml, which was calculated by soil porosity), and the groundwater level was maintained static for 12 h. In the quasistatic column (QSC), the groundwater level was maintained static throughout the experiments. In the natural fluctuation column (NFC) and rainfall infiltration column (RIC), three similar groundwater-level oscillation cycles were conducted using peristaltic pumps. Each cycle of groundwater-level oscillation includes several steps. Firstly, the groundwater level was raised from 40- to 80-cm height by injecting groundwater from column bottom over a period of 10 h at a flow rate 633 ml h^{-1} to simulate NF, while injecting rainfall water at the same flow rate from the top of column to simulate RI. The rainfall water was mimicked by tap water without any pretreatment, and the physical and chemical properties of the rainfall water are listed in Supplemental Table S2. Secondly, the groundwater level in both NFC and RIC was maintained static at 80-cm height for 40 h. Finally, the groundwater level in both NFC and RIC was dropped from 80- to 40-cm height by pumping groundwater out from column bottom at the flow rate 633 ml h^{-1} over a period of 10 h. The groundwater level was maintained static at 40-cm height for 40 h between cycles and for 12 h after the last cycle. The estimated pattern of groundwater level based on the flow rate of peristaltic pumps within NFC and RIC during the experiments is also shown in Figure 2 and Figure 3. For the NFC and RIC, the cyclic oscillations of groundwater-level created a 40-cm-thick oscillated zone between the vadose and unsaturated zone and the saturated zone. Therefore, we define 80- to 110-cm height as a vadose zone, 40- to 80-cm height as an oscillated zone, and 0- to 40-cm height as a saturated zone (Figure 1).

2.2 | Geochemical analysis

During the experiments, two TDR315L probes (Acclima) were placed in vadose and oscillated zone, respectively, to measure volumetric water content by a data collector

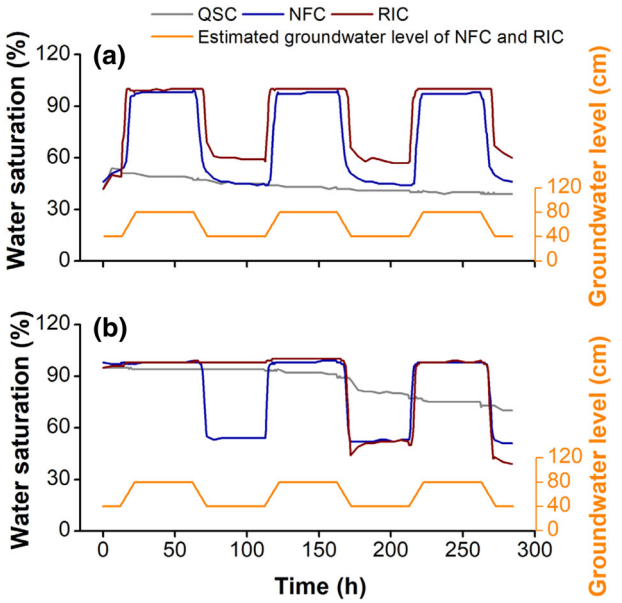

FIGURE 2 Spatiotemporal distribution of water saturation within the columns. Monitoring points are in the (a) vadose and (b) oscillated zones of the quasistatic column (QSC), natural fluctuation column (NFC), and rainfall infiltration column (RIC). Water saturation was monitored every half hour

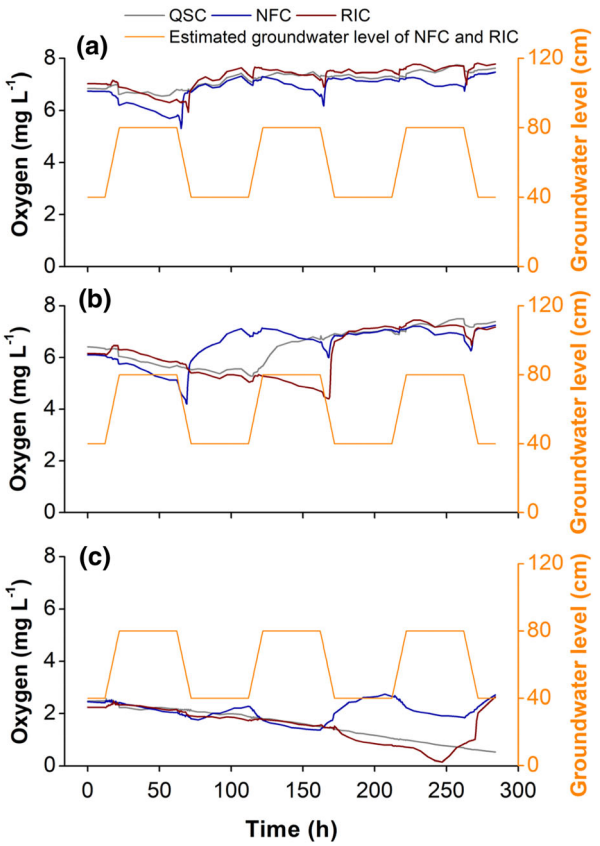

FIGURE 3 Spatiotemporal distribution of the O_2 level within the columns. Monitoring points are in the (a) vadose, (b) oscillated, and (c) saturated zones of quasistatic column (QSC), natural fluctuation column (NFC), and rainfall infiltration column (RIC). Oxygen level was monitored every half hour

CR300 (Campbell) (details can be found in the supplemental material). Water saturation was calculated by the ratio of measured volumetric water content with soil porosity. Three O_2 dipping probes (PreSens) were placed in the vadose, oscillated, and saturated zone, respectively. This was to measure the O_2 level by an OXY-10 trace SMA (PreSens) (details can be found in the supplemental material).

Groundwater samples in the saturated zone were collected from QSC, NFC, and RIC, each at 0, 12, 22, 62, 72, 112, 122, 162, 172, 212, 222, 262, 272, and 284 h after the start of the experiments. All groundwater samples were collected in triplicate, filtered through a 0.45-μm Millipore filter to remove solid particles, and then stored at 4 °C until further analysis. The details regarding dissolved organic C (DOC) and ultraviolet–visible measurement are described in the supplemental material.

At the end of the experiments, soil samples were collected from the vadose, oscillated, and saturated zones of QSC, NFC, and RIC each (more information can be found in the supplemental material). The soil samples collected from each zone were manually homogenized and divided into two parts. One part was dried naturally and passed through 100 mesh sieves. After removing inorganic C by acidification with 1% HCl, soil TOC was measured in triplicate using a Vario TOC system (Element) in the solid state at 950 °C. The other part was kept at −80 °C for the determination of soil bacterial community composition.

2.3 | Soil bacterial community analysis

Total DNA was extracted from 0.250 g of soil using a PowerSoil DNA Kit (MOBIO) following the manufacturer's instructions (Wang et al., 2019). The V3–V4 hypervariable regions of the bacterial 16S ribosomal RNA (rRNA) gene were amplified by polymerase chain reaction (PCR) with primers 338F (ACTCCTACGGGAGGCAGCAG) and 806R (GGACTACHVGGGTWTCTAAT) (Guo et al., 2018) (details can be found in the supplemental material). To reduce PCR errors, amplification for each sample was performed in triplicate and pooled together (Miao et al., 2017), and the amplicons were extracted from 2% agarose gels and purified by using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences) following the manufacturer's instructions (Wang, Bi, Hem, & Ratnaweera, 2018), and quantified using QuantiFluor-ST (Promega) (Liu, Wang, Guo, Zhao, & Zhang, 2018). The purified amplicons were sequenced on an Illumina MiSeq PE300 sequencer (Illumina) at Allwegene Technology Company (Beijing, China). Raw sequences were firstly selected based on sequence length, quality, primer, and tag (Yin

et al., 2019) (details can be found in the supplemental material). Alpha diversity analysis, including Shannon–Wiener curve (Supplemental Figure S2), Good's coverage, Chao 1, and Shannon indices, was calculated by the Mothur package (version 1.34.4). Subsequently, singletons were discarded to reduce the error rate with a small reduction in sensitivity (Zheng et al., 2019), and chimeric sequences were identified and removed using USEARCH (version 10). The high-quality sequences were assigned operational taxonomic units (OTUs) with 97% similarity (Liu, Wang, et al., 2018; Yin et al., 2019) using USEARCH (version 10). The OTUs were aligned with the Silva128 16S rRNA database using the Ribosomal Database Project (RDP) classifier (version 2.2) under the confidence threshold of 70% (Miao et al., 2017). Different taxonomic groups were classified using quantitative insights into microbial ecology (QIIME) package (version 1.2.1). The raw sequences have been deposited into the National Center for Biotechnology Information (NCBI) Sequence Read Archive under the Accession no. PRJNA573586.

2.4 | Statistical analysis

Significant difference in the soil TOC removal rates among different columns was assessed by one-way ANOVA using SPSS 20. Based on detrended correspondence analysis (DCA) result (gradient length <3.0), redundancy analysis (RDA) was selected to determine the multivariate correlations (Liu, Liu, et al., 2018) between bacterial community diversity, structure, water saturation, O_2 level, and TOC removal using Canoco 4.5. Pearson correlation coefficients were also calculated and tested for significance using SPSS 20.

3 | RESULTS AND DISCUSSION

3.1 | Spatiotemporal distribution of water saturation

For vadose zone, the water saturation in QSC increased in the first few hours of the experiments, then gradually decreased over the experimental period (Figure 2a). The increase in water saturation in first few hours is associated with the increase in the thickness of the capillary. The slight decrease in water saturation over the experimental period is probably due to evaporation within vadose zone (Kong et al., 2015). For NFC and RIC, water saturation was synchronously oscillated with the rise and fall of groundwater level (Figure 2a). However, the water saturation in RIC was higher than that in NFC, especially during the groundwater-level recession period. This is mainly attributed to the differences in the way the groundwater level was controlled. In RIC, the water harbored in the vadose zone was rainfall water that passed through the vadose zone to the oscillated zone. In contrast, the water harbored in the vadose zone of NFC was groundwater that sucked by the capillary forces, which was limited by gravity and the height of groundwater level (Hou, Li, Vanapalli, & Xi, 2019; Jost et al., 2015).

For the oscillated zone, the water saturation in NFC and RIC remained nearly stable from start to 62 and 162 h, respectively, and then periodically oscillated with the rise and fall of groundwater level (between 50.89 and 98.69%, and 39.49 and 100.00%, respectively) (Figure 2b). Compared with the cyclic oscillations of water saturation in NFC, the cyclic oscillations of water saturation in RIC was delayed for one cycle. However, substantial difference between NFC and RIC in each phase of the cyclic groundwater-level oscillations was practically nonexistent after the groundwater table increased to the highest level for the second time. This demonstrates that there is a time lag between RI and the rise in groundwater level during the early stage of rapid, short-term, cyclic, groundwater-level oscillations driven by RI (Batayneh & Qassas, 2006). The water saturation in QSC gradually decreased from 94.63 to 70.20% (Figure 2b), indicating that groundwater in the oscillated zone of QSC was sucked by the upper drier soil (Baram, Kurtzman, & Dahan, 2012) and lost by evaporation related to temperature and air flow (Chen et al., 2019) under hydrostatic groundwater level conditions.

3.2 | Spatiotemporal distribution of oxygen level

For the vadose zone, the change patterns of O_2 level are similar in all three columns (Figure 3a). The O_2 level in QSC remained constant in the first 70 h of the experiments, and then slightly increased to the end of the experiments. This is probably because of a temporal increase in diffusive O_2 flux from air to the soil pores when water saturation exhibited the opposite trend (Neale et al., 2000). Notice that although the temporal distribution of O_2 level displayed similar trends for NFC and RIC associated with different imbibition and drainage cycles, overall, O_2 level was lower in NFC than in RIC. This is because the infiltration of O_2–rich rainfall water resulted in additional supply of O_2 to the vadose zone of RIC (Kohfahl, Massmann, & Pekdeger, 2009), whereas the suction of O_2–depleted groundwater (Haberer, Roy, & Smith, 2015) led to the replacement of soil pore air and restricted the transport of air into the vadose zone of NFC (Dutta et al., 2015).

For the oscillated zone, the O_2 level in NFC and RIC oscillated accordingly with the rise and fall of groundwater level (Figure 3b). This oscillation was within 4.20–7.25 mg L^{-1} in NFC, and within 4.40–7.45 mg L^{-1} in RIC. However, the O_2 level in QSC decreased from 6.41 to 5.28 mg L^{-1} at 115 h, and then increased to 7.40 mg L^{-1}. The O_2 level of NFC oscillated over time with groundwater-level oscillations,

decreased as groundwater level rose, and increased as groundwater level dropped because the oscillated zone became a saturated zone with the rise of groundwater level. This could be explained by effective air contents, which were calculated by subtracting water saturation at a given location from the maximum effective porosity (McLeod, Roy, & Smith, 2015). Notably, the oscillations of O_2 level in RIC were one cycle later than those in NFC, due to the higher water saturation in RIC being able to provide significant resistance to O_2 transport and groundwater reoxygenation (Neale et al., 2000). The O_2 level in QSC decreased to the minimal value (115 h) and then gradually increased to the end of the experiments (Figure 3b) due to the effects of groundwater evaporation and reoxygenation.

For saturated zone, the O_2 level in QSC continuously decreased from 2.47 to 0.52 mg L^{-1}, whereas in NFC, it showed a continuous decline until ~80 h but an increase afterwards with a periodical oscillation between 1.38 and 2.71 mg L^{-1} (Figure 3c). For RIC, the long continuous decline in O_2 level was observed to be 0.15 mg L^{-1} at 247 h with a sharp increase to 2.63 mg L^{-1} in the end of the experiments. The continuous decrease of O_2 level in QSC indicates that the consumption of O_2 by organic C biodegradation or by other O_2 sinks in the soil was higher than the mass fluxes of O_2 replenished by advection and diffusion (Dutta et al., 2015). The periodical oscillations of O_2 level after ~80 h in NFC, returning to a similar level to the start of experiment, was probably due to the fact that O_2 was consumed by redox reactions, and reoxygenation could also occur due to oscillations in groundwater level (Davis et al., 2013), which could lead to diffusion and entrapment of air or soil air in the groundwater below groundwater level (Neale et al., 2000). Effective O_2 entrapment could likely contribute to the rebound of O_2 in the saturated zone, since mass transfer of O_2 has been reported in an oscillating capillary fringe even under a single drainage or imbibition event (Haberer et al., 2012). The oscillation of O_2 level in RIC, however, was two cycles later than that in NFC, which demonstrated that O_2 input to the saturated zone by RI was of minor importance, and even less than O_2 consumption by redox reactions in the saturated zone. This is because aerobic mineralization of organic C contained in the vadose and oscillated zones of RIC substantially consumed O_2 in rainfall water and air or soil air across the first two cycles (Datry, Malard, & Gibert, 2004). Interestingly, the last cycle showed a huge increase in the O_2 level, which might be due to the bacterial respiration-induced O_2 consumption decreasing as a result of labile organic C reduction after two cycles of groundwater-level oscillations, and more O_2 would be transported into the saturated zone. Although NF and RI appeared to have dissimilar effects on temporal distribution of O_2 level in the saturated zone, cyclic NF and RI were both significant hydrological dynamic events with respect to providing O_2 to the saturated zone compared with QS.

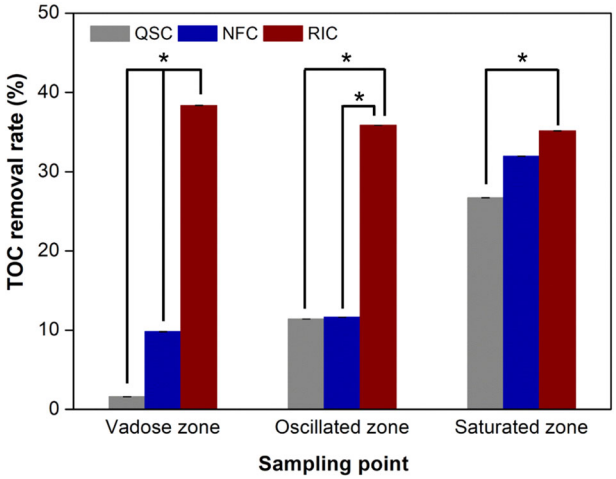

FIGURE 4 Variation in soil total organic C (TOC) removal at the end of the experiments as a function of depth. the error bars represent the standard deviation of the mean values. QSC, quasistatic column; NFC, natural fluctuation column; RIC, rainfall infiltration column. * Significant difference at $P < .05$

3.3 | Variation in total organic carbon removal with depth

The removal rates of soil TOC ranged from 1.60 ± 0.02 to 38.36 ± 0.04% across vadose zones ($p < .05$), from 11.42 ± 0.03% to 35.84 ± 0.01% across oscillated zones ($p < .05$) and from 26.71 ± 0.04% to 35.16 ± 0.04% across saturated zones ($p < .05$) (Figure 4). Among them, the vadose zone (38.36 ± 0.04%) and oscillated zone (35.84 ± 0.01%) of RIC achieved the highest TOC removal rates, followed by the saturated zones of QSC, NFC, and RIC. However, the removal rates of TOC in the vadose zone (1.60 ± 0.02%) and oscillated zone (11.42 ± 0.03%) of QSC were the lowest. This is because RI caused a considerable amount of rainfall water to flow through the vadose and oscillated zones and led to enhanced leaching, hydrolysis, biodegradation, and dissolution of soil organic C into soil solution (Gillefalk, Massmann, Nützmann, & Hilt, 2018) that transported into the saturated zone with groundwater level dropping (Chow, Tanji, & Gao, 2003).

The DOC concentrations in NFC and RIC exhibited cyclical responses, whereas the DOC concentration in QSC increased from 3.43 to 4.96 mg L^{-1} (112 h), and then decreased to 3.68 mg L^{-1} at the end of the experiments (Supplemental Figure S1a). It is worth noting that the DOC concentration of most groundwater sampled at specific time in RIC was lower than that in NFC. This demonstrates that DOC is likely to be mineralized by bacterial communities in the vadose and oscillated zones of RIC under aerobic conditions (Niu, Wang, Loáiciga, Hong, & Shao, 2017). The specific ultraviolet absorbance at 254 nm ($SUVA_{254}$) and the ration between the absorbance value at 253 nm and that at

203 nm (E_{253}/E_{203}) in NFC and RIC alternated between high and low values during rapid, short-term, cyclic, groundwater-level oscillations, with a downward trend in QSC (Supplemental Figure S1b). More importantly, ultraviolet absorbance at wavelengths of 200–300 nm exhibited higher values in RIC and NFC than QSC at the end of the experiments (Supplemental Figure S1c). Accordingly, we speculate that soil organic C acts as a great source of DOC, and only high molecular compounds that cannot be consumed by aerobic bacteria were left (Liu et al., 2019). Together with QSC, it is easy to judge from this study that the enhanced C cycle (such as leaching, dissolution, and biodegradation of soil organic C, and releasing and aerobic mineralization of DOC) occurred as a result of rapid, short-term, cyclic, groundwater-level oscillations and was especially driven by RI.

3.4 | Variation in soil bacterial community composition with depth

3.4.1 | Bacterial community diversity

For each sample, between 17,595 and 43,121 reads passed quality control (Supplemental Table S3). The coverage indices suggested that this was sufficient to give good coverage of the species present (Table 1, Supplemental Figure S2). In the vadose zone, the diversity indices (Chao 1 and Shannon) for RIC (RIC_V, where "V" stands for vadose zone) were slightly lower than those for NFC (NFC_V) and QSC (QSC_V) (Table 1). In the oscillated zone the diversity indices were very similar (RIC_O, NFC_O, and QSC_O), whereas in the saturated zone the bacterial community diversity of RIC (RIC_S) was higher than that of NFC (NFC_S) and QSC (QSC_S) (Table 1). The Venn diagrams illustrated that only 619 OTUs or 22% of the total OTUs were shared between QSC_S, NFC_S, and RIC_S (Supplemental Figure S3), suggesting a relatively high level of dissimilarity in bacterial communities. The number of OTUs unique to RIC_S (713) was much higher than those in QSC_S and NFC_S (309 and 292). Other researchers have demonstrated that soil bacterial community diversity can gradually decrease with significant removal of soil organic C by leaching, dissolution, and aerobic transformation (Ning et al., 2018). This could explain the diversity differences between the vadose zone communities, but not the similar diversity in the oscillated zone communities or that the highest diversity in the saturated zone was exhibited by RIC. Thus, our results suggest that other factors are also affecting diversity. For example, the downward infiltration of oxygenated rainfall water in RIC probably transports more nutrients to the saturated zone than in NFC or QSC, and this stimulates species diversity (Van Driezum et al., 2018).

3.4.2 | Bacterial community structure

To obtain detailed insights into bacterial communities, the phylogenetic classification of bacterial sequences from the vadose, oscillated, and saturated zones of three columns at two taxonomic levels (phylum and class) is summarized in Figure 5. The relative abundances of top 10 phyla are shown in Figure 5a. The composition of main bacterial communities was similar, and the most abundant bacteria belonged to the phylum Proteobacteria in all the samples (27.4–48.8%). Thus, it is concluded that the phylum Proteobacteria is highly adapted to a wide range of water saturation. This finding is consistent with previous reports indicating that Proteobacteria play a dominant role in aquifers (Unno et al., 2015). The phylum Acidobacteria was observed as a second abundant bacteria in the vadose and oscillated zones. Similarly, Gemmatimonadetes and Actinobacteria, which were reported to be usually present in upper soil with relatively low moisture (Huang et al., 2019; Zhou et al., 2019), were also more likely to be enriched in the vadose and oscillated zones. The phyla Firmicutes and Bacteroidetes exhibited higher abundances in the saturated zones of all three columns. Additionally, Firmicutes exhibited higher abundances in RIC (16.6%) and NFC (11.4%) than in QSC (8.8%), whereas Bacteroidetes exhibited higher abundance in QSC (11.9%) than in NFC (11.2%) and RIC (6.0%). A similar pattern to Bacteroidetes emerged when other bacterial communities, such as Parcubacteria or Verrucomicrobia, were considered.

The heat map of the top 20 abundant classes of soil samples is presented in Figure 5b. The dominant classes in the same zone of different columns were similar, but the distribution of bacterial community structure differed in the three zones. The dominant classes in the vadose zone were Alphaproteobacteria, Betaproteobacteria, and Gammaproteobacteria. The most abundant class in QSC, NFC, and RIC was Betaproteobacteria (11.6%), Betaproteobacteria (12.7%) and Gammaproteobacteria (14.8%), respectively. The dominant classes in the oscillated zone were Alphaproteobacteria and Betaproteobacteria. The relative abundance of Betaproteobacteria in QSC (10.5%) was lower than that in NFC (12.2%) and RIC (12.2%). The dominant class in the saturated zone was Betaproteobacteria, which exhibited similar abundance in all three columns (11.0–12.6%). This finding further revealed that Betaproteobacteria appear to be widely adapted to natural subsurface environments (Amano, Sasao, Niizato, & Iwatsuki, 2012) and are highly resistant to rapid short-term, cyclic, groundwater-level oscillations. The other dominant classes included Gemmatimonadetes, Sub_group6, Deltaproteobacteria, Sphingobacteriia, Bacilli, and Clostridia across the vadose, oscillated, and saturated zones of three columns. Among them, the relative abundance of Deltaproteobacteria was higher in the oscillated and saturated zones of all three columns and the vadose zone

TABLE 1 Bacterial community diversity indices

	Vadose zone			Oscillated zone			Saturated zone		
Index	**QSC**	**NFC**	**RIC**	**QSC**	**NFC**	**RIC**	**QSC**	**NFC**	**RIC**
Good's coverage	0.9546	0.9537	0.9587	0.9503	0.9495	0.9500	0.9539	0.9549	0.9443
Chao 1	1,978	1,999	1,854	2,188	2,207	2,173	1,954	1,917	2,316
Shannon	9.17	9.13	9.09	9.43	9.43	9.43	8.87	8.73	9.20

Note. QSC, the quasistatic column; NFC, the natural fluctuation column; RIC, the rainfall infiltration column.

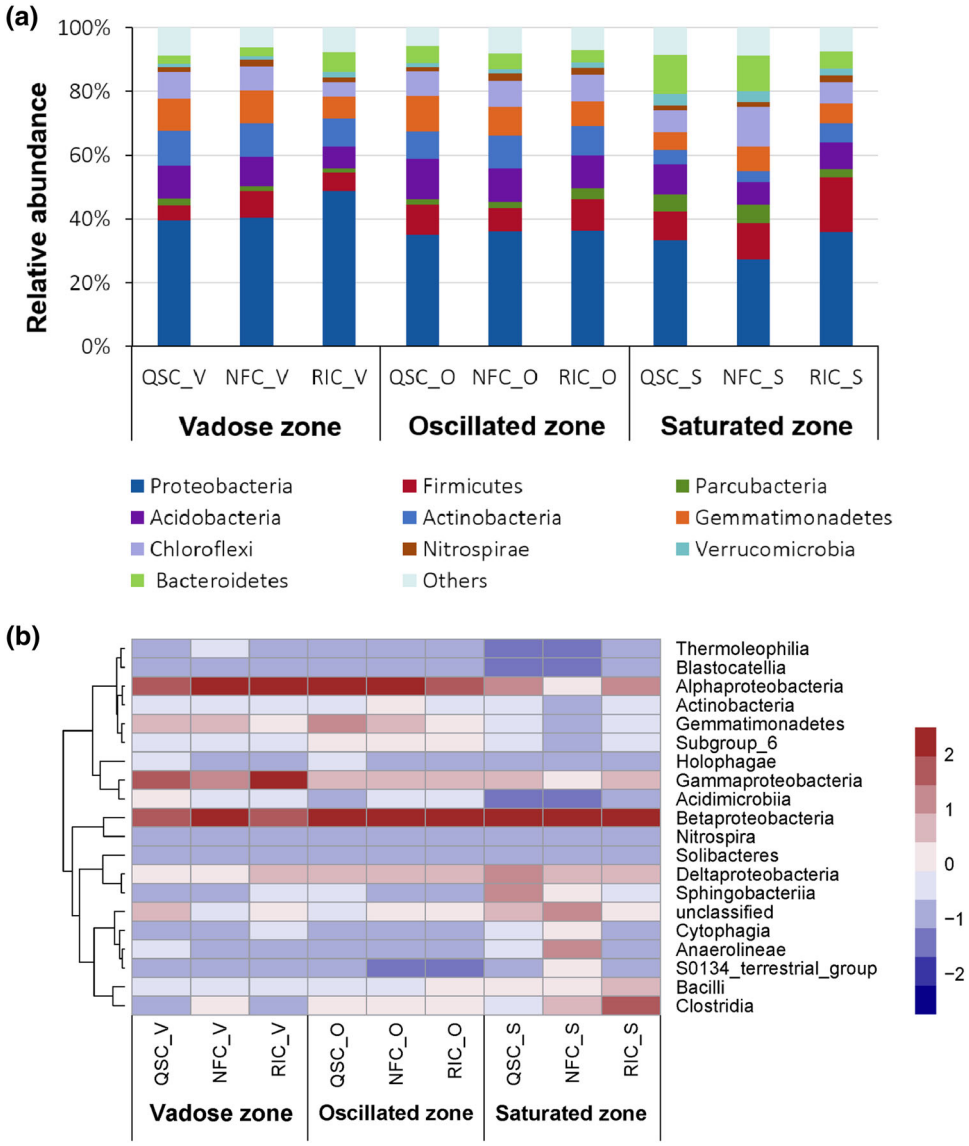

FIGURE 5 (a) Relative abundance of major bacteria at the phylum and (b) heat map of top 20 most abundant classes. The relative abundance is presented as the percentage of the total effective bacterial sequences in each sample. QSC, quasistatic column; NFC, natural fluctuation column; RIC, rainfall infiltration column. Labels "V," "O," and "S" indicate the vadose, oscillated, and saturated zones

of RIC. The dominance of Deltaproteobacteria is attributed to their special heterotrophic metabolic capabilities (Liu et al., 2019). That is the reason why Deltaproteobacteria were usually found in low TOC residual soils and likely contribute to soil TOC removal (Table 2).

It is worth mentioning that the classes Clostridia and Bacilli in the same phylum Firmicutes exhibited higher abundance in the saturated zone of RIC (10.4 and 6.5%, respectively) than in those of NFC (7.0 and 4.2%, respectively) and QSC (4.1 and 5.0%, respectively). Conversely, the Sphingobacteriia in the phylum Bacteroidetes exhibited higher abundance in QSC (7.6%) and NFC (4.7%). This might be because Firmicutes is one representative of heterotrophic bacteria related to labile organic C removal (Scheff, Salcher, & Lingens, 1984),

TABLE 2 Pearson correlation between geochemical parameters and bacterial communities

Community	Water saturation	O_2 level	TOC[a] removal rate
Betaproteobacteria	−.026	−.064	.423
Alphaproteobacteria	−.598	.676*	−.207
Deltaproteobacteria	.618	−.629	.827*
Sphingobacteriia	.857**	−.906**	.445
Gammaproteobacteria	−.526	.591	−.096
Bacilli	.650	−.682*	.437
Clostridia	.566	−.470	.426
Gemmatimonadetes	−.691*	.751*	−.786*
Cytophagia	.732*	−.580	.476
Actinobacteria	−.806**	.717*	−.641

[a]TOC, total organic C.

*,** Significant at the .05 and .01 probability levels, respectively.

whereas Bacteroidetes is more likely to mineralize recalcitrant organic C (Li et al., 2013). During the course of RI, more and more labile organic C is leached and transported to the saturated zone, and the bacterial communities that are able to biodegrade labile organic C still occupied a relatively high proportion. In contrast, the biodegradable organic C presented in the saturated zone of QSC and NFC tends to be refractory and should be biodegraded by other functional bacterial communities.

3.5 | Correlation between water saturation, oxygen level, total organic carbon removal, and bacterial community composition

Redundancy analysis was performed to assess how hydrological conditions induced geochemical conditions influence bacterial community diversity and bacterial community structure (Figure 6). Chao 1 and Shannon were chosen as diversity indices, and top 10 abundant classes were selected to analyze distribution of bacterial community structure in RDA ranking map. In the RDA ranking map, distribution of sample (bacterial community structure) is determined by correlations between the top 10 abundant classes and geochemical parameters. There is a negative correlation between TOC removal and Chao 1 and Shannon indices. Distribution of bacterial community structure in RIC_V, RIC_O, and the saturated zones of all three columns had a negative correlation with Chao 1 and Shannon indices as a result of greater TOC removal. This suggests the dominance of bacteria capable of decomposing organic C in specific ways that might replace the ecological niche of other bacterial communities (Zheng et al., 2019).

For classes, Gammaproteobacteria ($p < .05$), Alphaproteobacteria ($p < .05$), Actinobacteria ($p < .05$), and Gemmatimonadetes had positive correlation with O_2 level, Betaproteobacteria, Deltaproteobacteria ($p < .05$), Clostridia,

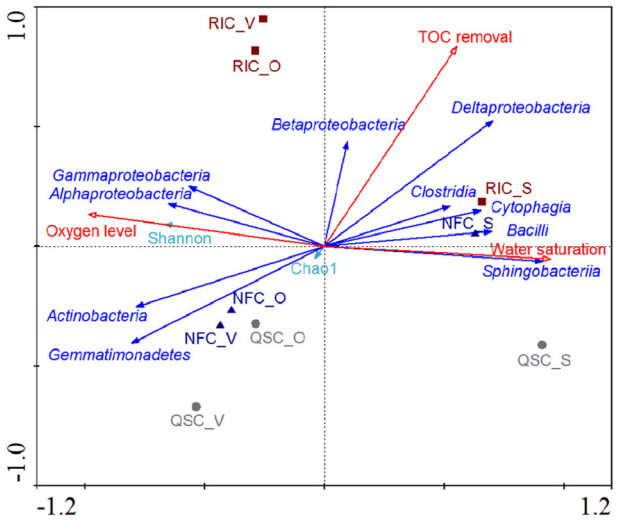

FIGURE 6 Redundancy analysis for the relationship between samples, bacterial community diversity, structure, water saturation, O_2 level, and total organic C (TOC) removal. Circles represent the quasistatic column (QSC), triangles represent the natural fluctuation column (NFC), and squares represent the rainfall infiltration column (RIC). Red arrows represent water saturation, O_2 level, and TOC removal. Cyan arrows represent bacterial community diversity indices. Blue arrows represent dominant bacterial species. Labels "V," "O," and "S" indicate the vadose, oscillated, and saturated zones

Cytophagia, Bacilli, and Sphingobacteriia had positive correlation with TOC removal, and Betaproteobacteria, Deltaproteobacteria, Clostridia, Cytophagia ($p < .05$), Bacilli, and Sphingobacteriia ($p < .01$) had positive correlation with water saturation. For samples, distribution of bacterial community structure varied in response to changes in water saturation, O_2 level, and TOC removal across the vadose, oscillated, and saturated zones of three columns. Distribution of bacterial community structure in the vadose and oscillated zones of three columns was positively related to O_2 level. Distribution of bacterial community structure in the saturated zones of all three columns was positively related to

water saturation. Distribution of bacterial community structure in the vadose and oscillated zones of RIC was positively related to TOC removal, whereas distribution of bacterial community structure in the vadose and oscillated zones of QSC and NFC was negatively related to TOC removal. Therefore, TOC removal is the driver of discriminating distribution of bacterial community structure in the vadose and oscillated zones of RIC from those of NFC and QSC. This demonstrates that TOC removal can be attributed to not only leaching and dissolution, but also biodegradation by bacterial communities (Kolehmainen, Langwaldt, & Puhakka, 2007). Moreover, distinct differences in TOC removal rates of the vadose and oscillated zones between NFC and RIC are related to the imbibition pathways, which affect the leaching and dissolution of organic C. Leaching and dissolution of organic C is a prerequisite for enhanced organic C biodegradation under dry–wet alternation condition during rapid short-term cyclic groundwater-level oscillations (Supplemental Figure S4). Overall, it can be concluded that rapid short-term cyclic groundwater-level oscillations driven by RI can significantly affect bacterial communities responsible for TOC removal in vadose and oscillated zones, whereas rapid, short-term, cyclic, groundwater-level oscillations driven by NF exhibit relatively low TOC removal rate and limit the responses of bacterial community structure.

Although bacterial community structure in the saturated zones of three columns were obviously different (Figure 5b, Supplemental Figure S3), O_2 level, TOC removal, and water saturation were not regulatory factors on the differences of bacterial community structure distribution. Other biogeochemical processes might occur through a series of transformation pathways (Lipson et al., 2012), which might account for the stimulation of diverse dominant bacterial communities under similar TOC removal rates in the saturated zones. Our results hint at a crucial role of RI in causing bacterial community structural responses and C cycle within vadose and oscillated zones during rapid, short-term, cyclic, groundwater-level oscillations.

4 | CONCLUSIONS

In this study, the effects of rapid, short-term, cyclic, groundwater-level oscillations on the spatiotemporal distribution of water saturation and O_2 level, removal rates of soil TOC, and soil bacterial community composition at different depths were analyzed. Water saturation and O_2 level exhibited similar patterns in NFC and RIC. Across the vadose, oscillated, and saturated zones, the TOC removal rates of RIC were higher than those of NFC and QSC. For the vadose and oscillated zones, bacterial community structures in RIC differed from those of QSC and NFC. Meanwhile, O_2 level was the dominant contributor for reshaping bacterial community structures in the vadose and oscillated zones of all three columns. However, water saturation had a positive correlation with distribution of bacterial community structure in the saturated zones of all three columns. Total organic C removal positively correlated with distribution of bacterial community structure in the vadose, oscillated, and saturated zones of RIC, as well as the saturated zones of NFC and QSC. Considering the patterns of TOC removal in the vadose, oscillated, and saturated zones of RIC, we speculate that rapid, short-term, cyclic, groundwater-level oscillations driven by RI could cause more possibility for leaching, dissolution, and biodegradation of soil organic C. These results suggest the importance of considering hydrological dynamic factors in the prediction of the impacts of rapid, short-term, cyclic, groundwater-level oscillations on soil bacterial community composition. Future studies should focus on the verification of the mechanisms linking functional bacterial communities to geochemistry by alternative means of detection.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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ORCID

Xuefeng Xia https://orcid.org/0000-0001-6251-7791

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