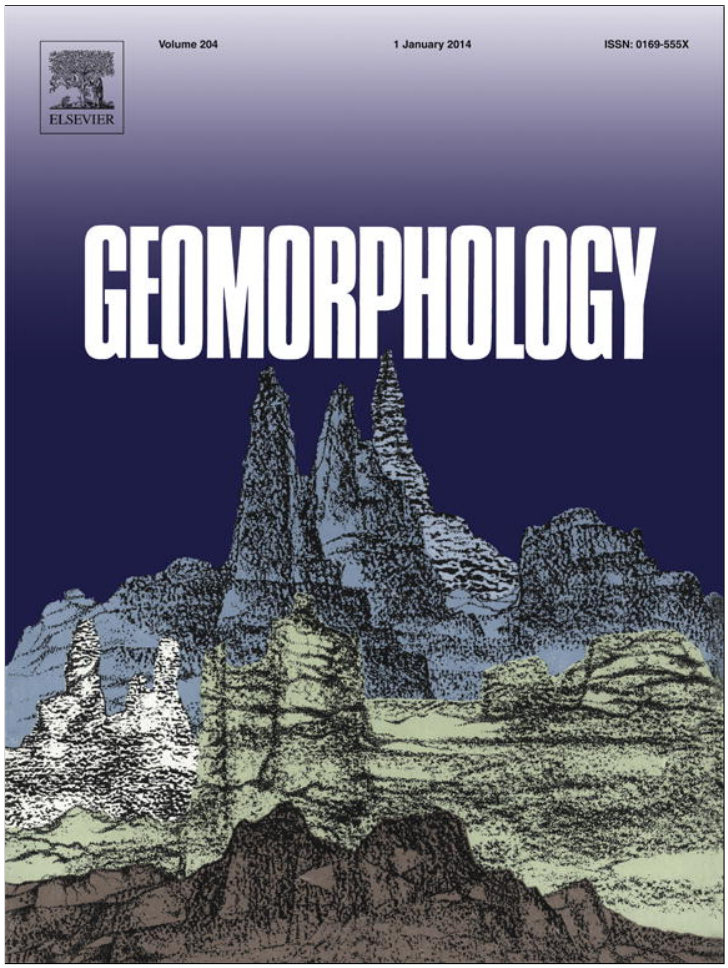

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Microbial responses to soil rewetting in erosional and depositional environments in relation to the organic carbon dynamics

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ABSTRACT

In order to investigate the microbial responses to soil rewetting in erosional and depositional environments in relation to organic carbon dynamics, three contrastive plots (in erosional, transitional, and depositional areas) were imposed with varying erosion or deposit characteristics in a typical sloping cropland of the red soil region in south China. The cropland was rewetted uniformly by a simulated rainfall under field conditions, and the three plots in the land were sampled before and 180 h after rewetting. Soil organic carbon (SOC) pools, DNA-based microbial abundance, and community structure were measured. In response to rewetting, the erosional area had greater microbial abundance than the transitional or depositional sites. The variations in bacterial and fungal abundance were not significantly correlated with the dynamics of soil carbon pools at site or during the whole experimental period. Bacterial diversity increased immediately after rewetting at downslope positions, especially in the depositional area. Fungal community structure was less sensitive to rewetting than that of bacteria and was rather dynamic at the erosional site compared with the depositional site. Together with site variables, the carbon data set significantly ($P < 0.01$) explained the variations of bacterial and fungal community structures after rewetting. To conclude, site erosion or deposit characteristics may affect the drying/rewetting (D/R) susceptibility of soil biogeochemical carbon cycles by inducing shifts in functional microbial communities with different responses to rewetting.

1. Introduction

Global, regional, and local carbon cycles can severely influence climate change, which has been widely studied for years (Cox et al., 2000; Lal et al., 2012). However, carbon dynamics in water-eroded soils remains poorly understood and quantified and thus is a key uncertainty in global carbon budgets (Lal, 2006; Lal and Pimentel, 2008; Boix-Fayos et al., 2009). Water erosion is coupled with changes in local soil properties and biological processes and can affect soil carbon dynamics through many complicated processes (Shi et al., 2010), including selective migration with runoff and sediment, mineralization conducted by soil microbial respiration, and enrichment and sequestration in the depositional area (Lal, 2005). In fact, the fate of eroded soil organic carbon (SOC) or the dynamics of reserved carbon in erosional sites is closely related to soil microorganisms as they mediate critical carbon transformations (Carney et al., 2007). This pattern is strongly regulated by environmental stressors and perturbations, e.g., soil drying and rewetting (D/R) (Gordon et al., 2008), which will subject soil microbes to physiological stresses by decreasing substrate diffusion and thus lead to changes in metabolism (Schimel et al., 2007).

Water erosion exposes SOC and releases soil microorganisms that are physically protected within aggregates in erosional areas. Selective transpositions induced by runoff will then drive soil carbon and soil particles to be redistributed in the landscape (Chartier et al., 2013; Shi et al., 2013). Finer particles and associated SOC are preferentially transported away from eroding slopes to low-lying depositional environments (Berhe et al., 2007), which creates different habitats for soil microorganisms in erosional and depositional environments. In an erosional environment, coarse soil particles remain in situ and restrict soil aggregation. As a result, SOC is exposed to microbial attack and gradually mineralized to CO_2 owing to lack of protection (Lal, 2005). In contrast, in a depositional environment, abundant substrate and suitable temperature/moisture conditions may benefit soil microorganisms and aggregate formation, which will profoundly increase the soil organic matter (SOM) turnover and perhaps SOC sequestration (Renwick et al.,

Abbreviations: D/R, drying/rewetting; SOC, soil organic carbon; SOM, soil organic matter; DOC, dissolved organic carbon; EA, erosional area; TA, transitional area; DA, depositional area.

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2004). The breakup of initial soil aggregates at erosional sites and the erosion during transport may be responsible for increased microbial mineralization and CO_2 emissions, while encapsulation of SOC within soil aggregates may be a major limitation to its microbial decomposition in a depositional environment (Polyakov and Lal, 2008). Ultimately, all these mechanisms involved in soil carbon turnover are affected by D/R perturbation.

Similar to the Mediterranean ecosystems (Boix-Fayos et al., 2009), many areas of the red soil region in south China also suffer from frequent D/R and serious erosion caused by climate change and poor management. We recognize that D/R stressors have remarkable effects on microbial physiology and community composition, which imply the carbon turnover and nutrient flow in terrestrial ecosystems (Schimel et al., 2007; Gordon et al., 2008). However, the effects of D/R on soil structure (i.e., aggregation) as well as soil microorganisms in erosional and depositional environments are still unclear and may be an important mechanism that controls the carbon turnover in these two environments. In fact, soil aggregate dynamics and its relationship with microbial community were suggested as key controlling factors on SOC dynamics, and D/R cycles may enhance aggregate turnover and SOM decomposition (Denef et al., 2001).

Most studies on SOC dynamics and carbon sequestration in relation to soil erosion focus on migration and redistribution during erosion, but not on the fate of in situ and eroded carbon that was intercepted and captured within the landscape after erosion. Moreover, organic carbon is lost from soil mainly through mineralization into CO_2 (Gregorich et al., 1998), and this pathway is closely associated with soil microorganisms. However, few studies are concerned with the variation of microbial community composition in response to rewetting within eroded sloping croplands or how these dynamics can profoundly influence carbon turnover. Therefore, the aims of this paper are to (i) report the changes in SOC stock and microbial community composition (including abundance and community structure) induced by rewetting over a period of 180 h, and (ii) evaluate the relationship between microbial community composition and SOC dynamics in response to rewetting at three sites with different erosion degrees and deposit characteristics within a typical sloping cropland.

2. Materials and methods

2.1. Experimental site

The experiment was conducted at a Soil and Water Conservation monitoring station (111°22′ E., 27°03′ N.) located in the Shuangqing district in Shaoyang City of Hunan Province, in the hilly red soil region of south China (Fig. 1). The study area is in a subtropical monsoon climate zone, with annual mean minimum and maximum temperatures of 16.1 and 17.1 °C, respectively. Mean annual precipitation is 1327.5 mm, 55% of which occurs from May through August, the months of the rainy season. In summer, with high temperatures and frequent high intensity thunderstorms, this area is subjected to serious water erosion and periodic D/R. The soil type is typically Quaternary red clay, with clay-to-loam texture. The U.S. Soil Taxonomy classified the soils as Ultisols.

The experimental site, a typical sloping cropland, was planted with *Polygonatum odoratum* (Mill.) Druce for 10 years until 2009 and then left unused until the experiment was performed on 15 July 2011. The farming method for this land was chisel plow. Above-ground biomass of crops was typically stacked at the top of the sloping land to avoid being flooded after digging the root block, which might raise carbon content in surface soil. The sloping cropland consists of closely dissected short and steep slopes in lengths of 1–3 m and gradients between 5% and 15% (Fig. 2B). As such, erosional and depositional environments were delineated and water and eroded sediment from the erosional area were rapidly directed downslope where reduced slope gradient would decelerate and obstruct the sediment-laden runoff water, and thereby induce deposition.

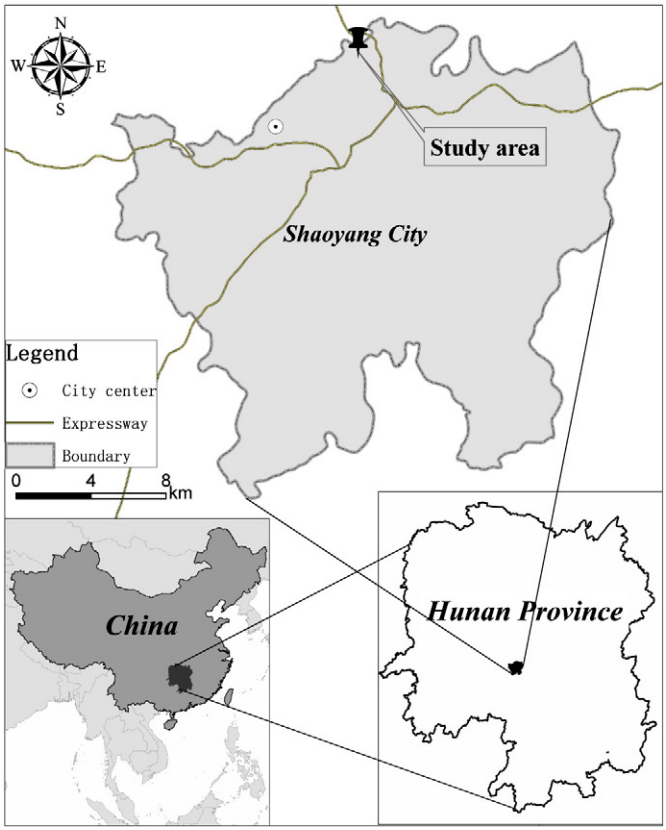

Fig. 1. Location of the study site.

2.2. Experimental design

The experiments were carried out in the summer of 2011 (15–22 July) and lasted 180 h. A block (2 m wide × 5 m long) was taken from the selected sloping cropland using metal frames. The block was divided into five equivalent plots A, B, C, D, and E (2 m × 1 m) along the slope. Plots A, C, and E were chosen as experimental treatments and sampling sites according to their erosional or depositional characteristics within the cropland (Fig. 2A). From the perspective of topography,

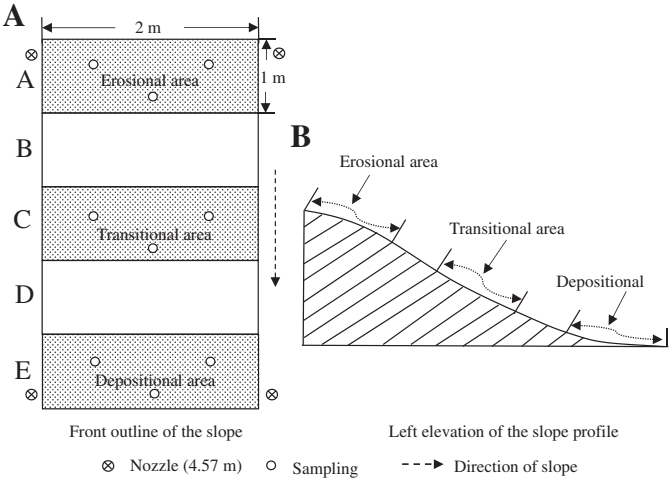

Fig. 2. Design of plots and sampling sites for rewetting by rainfall simulation.

many studies (McCarty and Ritchie, 2002; Papiernik et al., 2005) suggested that upslope positions are generally eroded areas, while lower slope positions are generally depositional ones. In addition, because of the selective transport conducted by runoff (Brackley et al., 2010), larger grain material (e.g., sand and gravel) is generally higher in eroded and nondepositional areas compared with depositional areas; but the opposite is true for fine grain material (e.g., clay) (Hall et al., 2013). Plot A, which was located at the upper part of the slope and had the highest sand content among the five plots (Table 1), should be a typical erosion area (EA). In contrast, plot E, which was located at the footslope part where the slope gradient was obviously slowed down (Fig. 2B) and a large amount of fine eroded material was deposited (Table 1), was proved to be a typical deposition area (DA). Plot C – which was located at the middle part of the slope, suffered soil erosion, and meanwhile received the eroded sediment from upper slope – was designed as the transition area (TA). In fact, the length of the experimental cropland is only 5 m and the average gradient of the slope is merely 10%, which decelerates the velocity and energy of runoff and thereby induces deposition readily within the slope.

Prior to rainfall simulation, the litter, plant residue, and some other debris brought into the experimental land were removed from soil surface. The rainfall simulation was conducted from 7:00 AM to 7:30 AM on July 15. The duration of the rainfall event was mainly determined by two reasons: (i) to thoroughly rewet the experimental block and (ii) to avoid generating surface runoff that could induce water erosion. In order to uniformly rewet the block, a rainfall simulator with a SPRACO cone jet nozzle mounted on the top of fixed stand pipes, 4.57 m in height, was located at the borders of the block to generate homogeneous rainstorms (Fig. 2A). The median drop size was 2.4 mm with a uniformity of 89.7%, and the intensities were 0.5–0.7 mm min^{-1}. No visible erosion was detected within the slope during the rainfall. A period of several hours (e.g., 24 h) after rewetting is expressed as 24 h.

2.3. Sampling schedule

All three plots were sampled at the 0–10 cm layer using a 70-mm (1.25-in.) diameter push probe to measure soil properties, SOC, dissolved organic carbon (DOC), and microbial community composition (i.e., abundance and community structure) dynamics, respectively. In each area, three separately arranged grids (20 cm × 20 cm) were chosen as the three replicates (Fig. 2A). Subsamples were taken from the three grids for physicochemical parameters measurement, and the same amount of soil taken from each of the three subsamples were finally mixed as the sample of the plot for DGGE analysis. All samples were labeled and sealed in air-tight Ziploc bags and stored instantly at −20 °C before use. The sampling was conducted before the simulated rainfall experiment and then at 24, 60, 108, 156, and 180 h intervals afterward.

2.4. Measurements

2.4.1. Measurement of physicochemical parameters

Prior to conducting SOC measurement, soil samples were pretreated by vacuum freeze drying at −60 °C and 6 Pa for 36 h. The freeze-dried soil samples were then used for SOC analysis. The SOC was determined using the dichromate oxidation of Walkley and Black (1934). The DOC was measured with a soil extract (water to fresh soil sample ratio of 10:1) in a Total Organic Carbon Analyzer (TOC-V_{CPH}, Shimadzu, Japan) after centrifuging at 12,000 rpm for 15 min and filtering through a 0.45 μm membrane filter. A soil-to-water ratio of 1:10 (*w*/*v*) was used for measuring soil pH with a digital pH meter (Woonsocket, RI, USA). Soil particle size analysis was calculated with the pipette method (Gee and Bauder, 1986). Three replicates were used in SOC and DOC analysis.

2.4.2. DNA extraction, qPCR and PCR-DGGE

Total DNA was extracted from the freeze-dried soil samples (~8 g) according to the method described previously (Yang et al., 2007). After purified with a Purification Kit (Bioteke, Beijing, China), the extracted DNA was dissolved in 100 μL of TE buffer and stored at −20 °C before use. Primers 338f and 518r as well as NS1 and Fung were used for the quantification of bacterial and fungal community gene abundance, respectively. The qPCR was conducted by the method of Zeng et al. (2011).

The bacterial 16S rDNA gene and fungal 18S rDNA gene for PCR-DGGE were amplified using primers 338f and 518r as well as Fung and NS1, with the forward primers (i.e., 338f and Fung) attached by a GC clamp to prevent complete separation of the DNA strands during DGGE. Mixture preparation and PCR amplification procedure design were conducted as described by Zhang et al. (2011). Electrophoresis was performed in a 1 × TAE buffer at 60 °C, 80 V for 12 h. After being stained with Du-red nucleic acid gel stain, the gels were scanned and analyzed with QuantityOne software V2.0 (Bio-Rad, Hercules, CA, USA).

2.5. Data analysis

The microbial abundance (i.e., gene copies per gram of dry soil) was normalized, if required, prior to analysis using $\log_{10}$ transformations. The DGGE bands with relative intensity (i.e., rDNA gene relative-abundance) below 1% were excluded from the analysis. For each parameter of microbial abundance as well as soil carbon data set, a one-way analysis of variance (ANOVA) was performed to compare their mean values for different sites or sampling time points and to test whether there were any significant differences among the means at the 95% confidence level by SPSS (version 11.5). Bivariate correlation analysis by SPSS (version 11.5) was used to detect the correlation between microbial populations and soil carbon pools after rewetting. Direct multivariate analyses, including principal components analysis (PCA) and redundancy analysis (RDA), were widely used to relate changes in community composition to changes in the environment and to provide statistical tests for these correlations (Zhang et al., 2011). Based on Canoco (version 4.5, Centre for Biometry, Wageningen, The Netherlands), PCA was performed separately to better detect spatiotemporal differences of bacterial and fungal community structure data since rewetting. The RDA was adopted to analyze the relationship between microbial community structures of soils derived from different areas of the experimental sloping cropland. It was also conducted to test the hypothesis whether the microbial community structures were significantly related to soil carbon dynamics under the influence of rewetting dry soils of erosional and depositional areas. Partial RDA was used to extract the variation in soil microbial community structure explained by each of the environmental explanatory variables or their sets (i.e., soil carbon data set or site data set) without synergic action with others, as well

Table 1
Soil properties (0–10 cm) of the erosional (EA), transitional (TA), and depositional (DA) soils; values are mean ± standard error, n = 3; values with the same letters are not significantly different at the $P < 0.05$ level as determined using an LSD test in one-way ANOVA model by SPSS 18 version.

	Soil organic carbon (g C kg^{-1} dry soil)	pH	Soil texture (%)		
			Clay	Silt	Sand
EA	8.81 ± 0.21^{a}	4.88 ± 0.01^{a}	31.27 ± 0.78^{b}	29.41 ± 1.93^{a}	39.32 ± 2.63^{a}
TA	5.88 ± 0.54^{b}	4.95 ± 0.02^{a}	35.08 ± 0.52^{a}	29.28 ± 2.85^{a}	35.64 ± 2.78^{c}
DA	4.54 ± 0.21^{c}	4.90 ± 0.01^{a}	37.12 ± 0.76^{a}	24.21 ± 5.97^{b}	38.67 ± 6.11^{b}

as the variation shared by these variables or sets. Monte Carlo reduced model tests with 499 unrestricted permutations were used to evaluate the significance of the first canonical axis and of all canonical axes. All of the analyses were conducted at the $P < 0.05$ level.

3. Results

3.1. Total SOC and DOC dynamics

Total SOC content (Fig. 3A) before rewetting (0 h) changed in the order as EA > TA > DA, and it was significantly higher in EA than in TA and DA ($P < 0.01$). From 0 to 24 h, SOC contents in EA (decreased by 17.6%, $P < 0.001$) and DA (increased by 20.5%, $P < 0.001$) responded strongly to the simulated rainfall but did not change significantly in TA ($P > 0.05$). From 24 to 60 h, SOC were relatively stable for all treatments. Over the 96 h after 60 h, SOC remained stable in DA, whereas it fluctuated oppositely in EA to that of TA. The SOC dynamics in TA and DA after 108 h were highly similar to that in EA after 60 h.

Prior to rewetting (0 h), DOC changed in the order as TA > EA > DA (Fig. 3B). The DOC declined by 60 h in all soils and was about 15% lower than that before rewetting. After the trough at 60 h, DOC began to increase in EA and TA until 156 h, and then reached 1.43 and 1.29 times higher than those at 60 h, respectively. The DOC was more stable in DA than TA or EA, though DOC dynamics in the three plots showed similar response patterns before 156 h. However, from 156 h to the end (180 h), DOC in EA and TA began to decrease again; but in DA, it continued to increase and was 31.8% higher than that at 60 h. At 108 h, DOC in EA exceeded that in TA and stayed at the highest level among the three areas until 180 h ($P < 0.001$).

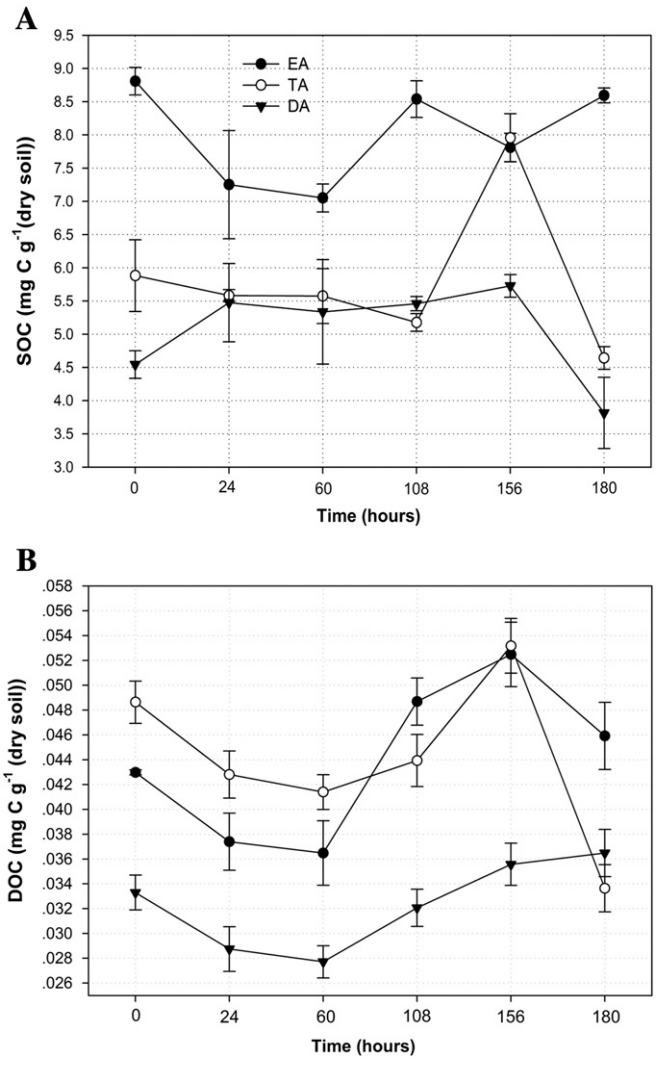

Fig. 3. Total soil organic carbon and dissolved organic carbon in dry soil (0 h) and in soils from 24 to 180 h after rewetting for the erosional (EA), transitional (TA), and depositional (DA) areas. Error bars represent the standard error of the means.

3.2. Microbial response

3.2.1. Microbial abundance dynamics in response to rewetting

The total microbial abundance had similar dynamic patterns as bacterial, indicating that after rewetting bacteria were absolutely superior over fungi in populations (Fig. 4A and B). After a long dry period before rewetting (0 h), no differences in either bacterial abundances or fungal abundances were detected among the three slope positions. During the 180 h after rewetting, fungi were more dynamic than bacteria in abundance because the abundance variations over time were especially evident for fungi.

Bacterial abundance of the three plots (Fig. 4A) increased significantly until 156 h and then decreased until 180 h ($P < 0.05$), except that abundance in TA fluctuated between 60 and 156 h. However, from 0 to 24 h, bacterial abundance of TA increased significantly by 14.2% ($P < 0.05$), but no dramatic changes were observed in EA or DA ($P > 0.05$). Intersite differences in bacterial abundance were more pronounced at 24 h than 0 h, and it was about 13.9% higher in TA than DA ($P < 0.05$).

After rainfall simulation, fungal abundance (Fig. 4B) decreased immediately in DA and was 20.7% lower ($P < 0.001$) at 24 h than at 0 h. In contrast, abundance did not change appreciably in EA or TA within the initial 24 h. From 24 to 60 h, fungal abundance decreased significantly in TA ($P < 0.05$), but increased significantly in DA ($P < 0.05$); still no significant change was detected in EA ($P > 0.05$). After 60 h, the fungal abundance of all three areas increased until 156 h and then gradually decreased until the end. Similar to bacterial, fungal abundance did not differ significantly among the three soils throughout the experiment, except that it was significantly lower ($P < 0.001$) in DA than in EA or TA at 24 h. However, unlike bacteria, intersite differences in fungal abundance were not significant between the dry and moist soils at 156 h ($P > 0.05$).

3.2.2. Microbial community structure variation in response to rewetting

Microbial community structures were very dynamic after rewetting, as severe shifts in the DGGE profiles were observed between the sampling sites and between time points (Fig. 5). Bacterial and fungal community structure data were analyzed separately using PCA to reveal spatiotemporal differences after rewetting. General dissimilarities were represented by the scattered pattern of data points. For bacteria, PCA clearly separated EA and DA, while substantial overlap was detected between TA and DA (Fig. 6A). In dry soils, no remarkable differences in bacterial community structure were observed among the three soils, as the samples of the three areas were clustered at 0 h (Fig. 6A). From 0 to 24 h, changes of bacterial community structure were more pronounced in EA than in TA or DA. However, after the rainfall simulation, bacterial community structure in EA was less dynamic than those in TA or DA, as evidenced by the fact that EA samples were grouped together while EA and TA samples scattered. Over the experiment, the variations of bacterial community structure in the three treatments were most pronounced within the initial 24 h. Bacterial community structures measured in dry soils from the three areas were evidently different from those in the wetter soils (Fig. 5A).

For fungi, PCA revealed no remarkable differences in community structure between EA and DA in the dry soils (Fig. 6B). However, after rewetting, the dissimilarities between data points of the two plots enlarged immediately, as the fungal community structures in these two treatments showed obviously different patterns at 24 and 60 h (Figs. 5B and 6B). As bacteria, the community structure of fungi was

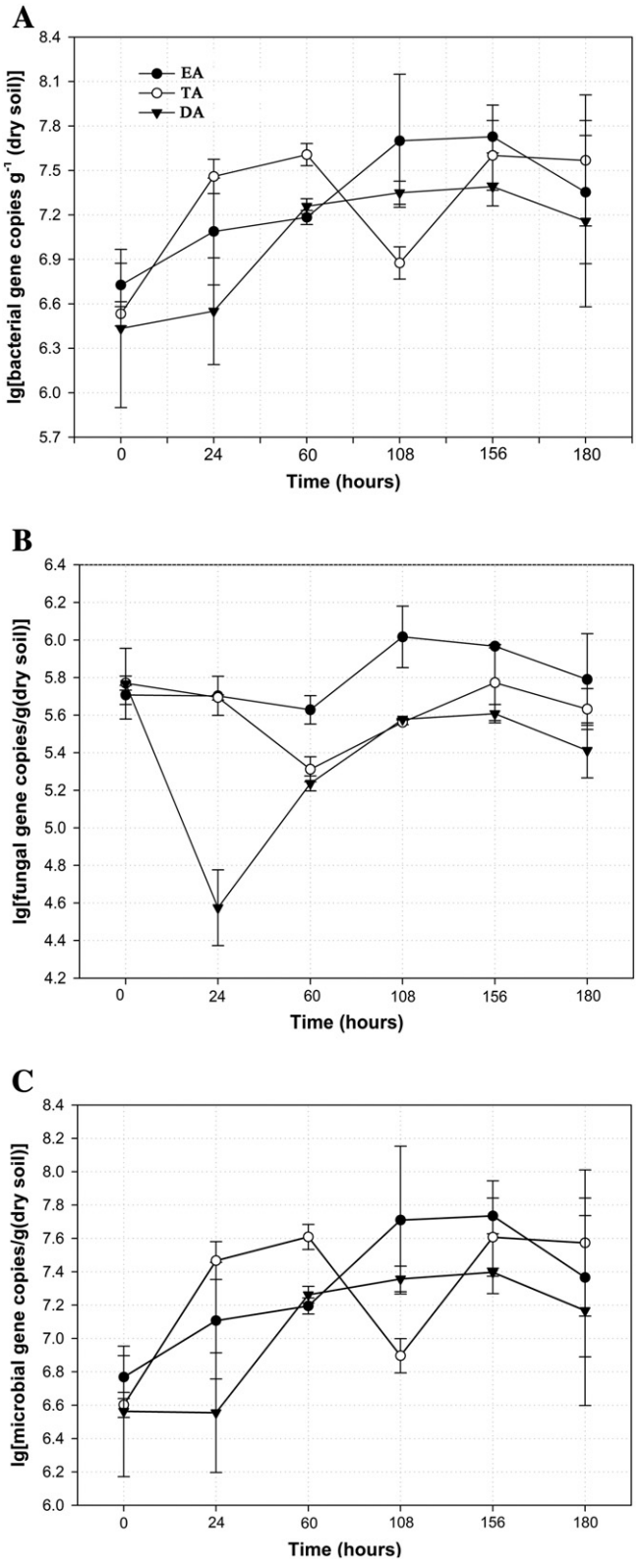

Fig. 4. Bacterial and fungal abundance in dry soil (0 h) and in soils from 24 to 180 h after rewetting for the erosional (EA), transitional (TA), and depositional (DA) areas. Error bars represent the standard error of the means.

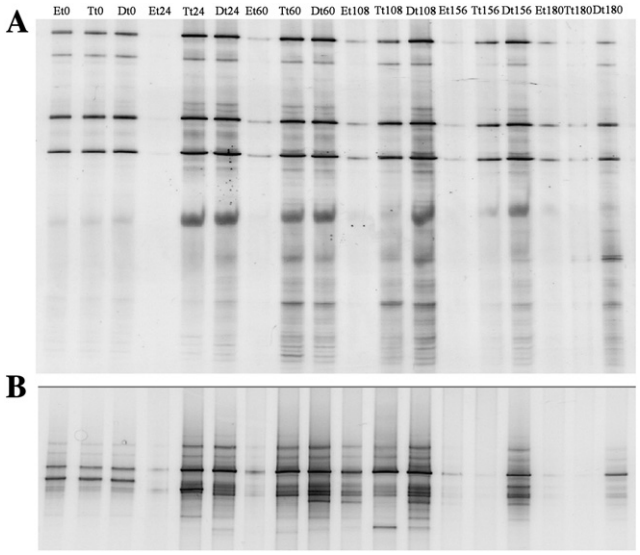

Fig. 5. The DGGE profiles of amplified bacterial 16S rDNA (A) and fungal 18S rDNA (B) fragments from the dry and rewetting soil samples. The numbers refer to the sampling days. The initials D, E, and T followed with sampling hours (t0 indicating dry soil, t24, t60, t108, t156, and t180 indicating 24, 60, 108, 156, and 180 h after rewetting, respectively) indicate erosional, transitional, and depositional areas, respectively.

more dynamic in EA than in DA under the influence of rewetting; this measure in TA was most sensitive to rewetting among the three treatments. Compared with bacteria, the effects of rewetting on fungal community structure were more remarkable, which can be seen by the scattered pattern of data points in the bi-plots; PCA bi-plots are considerably more scattered for bacteria than for fungi (Fig. 6A and B).

During the sampling period, a total of 33 types of bacteria and only 10 types of fungi genes (i.e., species) were detected by DGGE in the three plots (Figs. 5B, 6C and D). In order to investigate the response of specific species to rewetting in different areas of the slope, a PCA-based species and environmental variables bi-plot diagram was generated to probe into the bacterial and fungal community structures across the slope (Fig. 6C and D). The relative position of the projection point of the plot points on a given species vector line represents the relative abundance of this species in the plot. Most bacterial species were observed in TA and DA, but were more abundant in DA than in TA; whereas only four bacterial species were dominant in EA (Fig. 6C). With respect to fungi, the relative abundances of most species were highest in DA, while only a few species could proliferate abundantly in EA or TA (Fig. 6D).

3.3. Correlation between microbial community structure and soil carbon

Bivariate correlation analysis (data not shown) indicates that only bacterial populations decreased and were correlated negatively with DOC in EA and TA within the initial 60 h after rewetting, while no significant correlation ($P > 0.05$) between fungal gene abundance and soil carbon content was detected at any temporospatial scales in this study.

For bacterial community structure RDA (Fig. 7A), the environmental data together could explain 66.3% of the variation (Monte Carlo permutation test with 499 permutations, $P = 0.002$) and joint effects of other environmental data, SOC, and DOC could explain up to 46.0% of the variation (Monte Carlo permutation test with 499 permutations, $P = 0.002$). However, partial RDA showed that the variation explained by the soil carbon data set (SOC and DOC data combination) alone was not significant (Monte Carlo permutation test with 499 permutations, $P = 0.218$), which suggested that the significant contribution of soil carbon data sets was largely caused by combined effects with other variables, such as site erosion or deposit characteristics.

The correlation structure between fungal community structure dynamics and environmental data is summarized in Fig. 7B. All the environmental variables could jointly explain 53.2% (Monte Carlo

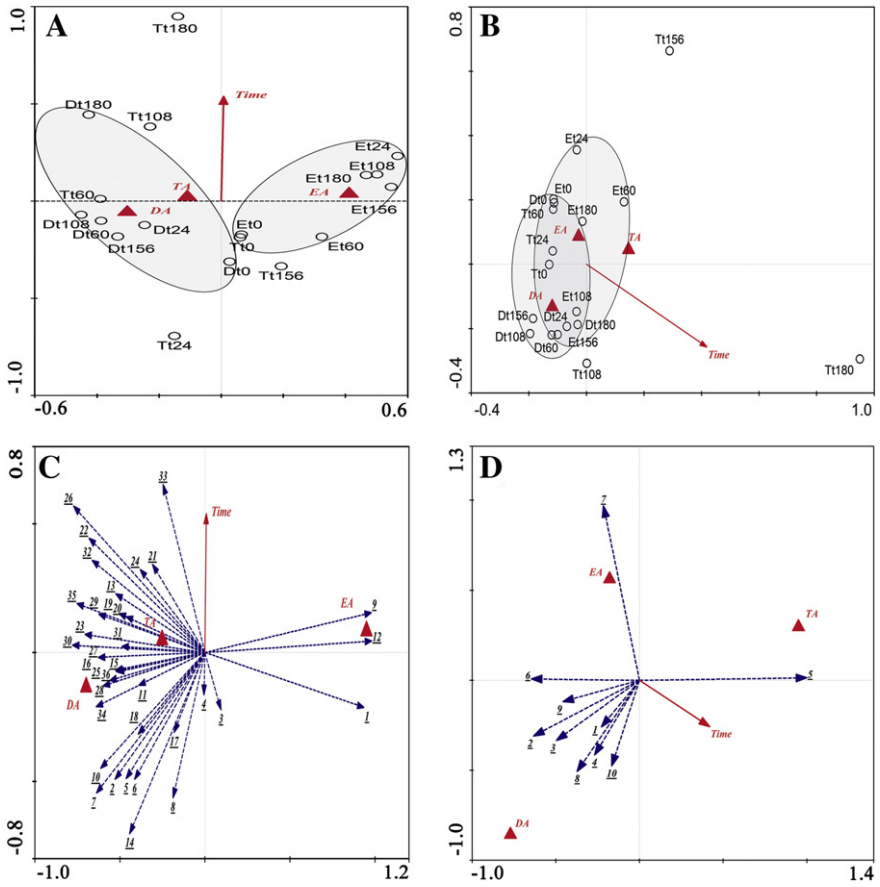

Fig. 6. Principal components analyses (PCA) for bacterial (A) and fungal (B) community structure. Environmental parameters with Pearson correlation of $R > 0.5$ are shown by a triangle (i.e., nominal variables are designated by EA, TA, or DA for erosional, transitional, or depositional areas) or solid lines with filled arrows. Samples are represented by open circles. The initials D, E, and T followed by sampling hours (t0 indicating dry soil, t24, t60, t108, t156, and t180 indicating 24, 60, 108, 156, and 180 h after rewetting, respectively) indicate erosional, transitional, and depositional areas, respectively. In *bacterial* (C) *and fungal* (D) *species and environmental variables* bi-plot diagrams based on PCA, species parameters are shown using dashed lines with filled arrows. Each species parameter indicated by a number represents the total rDNA gene relative abundance of this species.

permutation test with 499 permutations, $P = 0.006$) of the variation, and SOC and DOC together could explain up to 21.9% of the variance without sharing effects with other environmental data (Monte Carlo permutation test with 499 permutations, $P = 0.04$).

4. Discussion

4.1. Soil microbial response and carbon dynamics after rewetting

The D/R caused an immediate increase in the size of total microbial populations in all soils, which is consistent with Williams and Rice (2007) who found that microorganisms increased after the soil dried for 14 days was rewetted. In our study, bacterial and fungal abundances showed dissimilar responses to rewetting during the early period. Bacterial abundances in the three soils generally increased after rewetting and reached the greatest levels at 156 h. The increase in bacterial growth could be explained by increased growth of a small number of dormant bacteria growing on a substrate becoming more available after rewetting (Iovieno and Bååth, 2008).

In contrast, as described by Gordon et al. (2008), we found that D/R caused varying degrees of fungal abundance reduction among the three soils. The fungal population of the three soils gradually decreased to its lowest level from 0 to 60 h, indicating that fungal abundance is more sensitive to D/R than bacterial abundance. This finding probably resulted from the fact that soil fungi, which are located in/on the outer part of soil aggregates (i.e., in the larger pores and on aggregate surfaces), are thus more susceptible to rewetting than the microorganisms that are located within small pores dominated by bacterial populations (Grayston et al., 2001). Rewetted soil allows bacteria, especially Gram-negative bacteria groups, to prevail and mineralize available organic carbon and nitrogen sources, as the growth of such groups is strongly controlled by the input of labile carbon sources (Iovieno and Bååth, 2008). This observation is consistent with our finding that bacterial groups contributed to most of the total microbial populations in rewetted soils and that the bacterial abundance rather than fungal abundance could benefit from D/R. This observation is also supported by another finding of this study that DOC, as one of the most active components of labile carbon sources and an important substrate that can be directly utilized by microorganisms, was immediately reduced and showed negative correlations with bacterial populations in EA and in TA from 0 to 60 h after rewetting.

Microbial community structure, measured by DNA-based DGGE method that could reveal changes in relative abundance of certain species (e.g., within bacterial or fungal groups), also showed different dynamics between these two groups after rewetting. Chowdhury et al. (2011) found that the microbial community structure was not as susceptible to soil rewetting as microbial abundance. However, the PLFA method they adopted is only a relatively coarse measure of community structure because it cannot provide information at species or genotype levels. Based on the rDNA method, we found that bacterial community structure was more dynamic than fungal community structure after rewetting. Some studies (Harris, 1981; Fierer et al., 2003) suggested that soil D/R stress has a strong selective function on microbial diversity, so species that cannot adapt to this disturbance would die out. For example, repeated changes in soil water potential might favor some fungal groups (Huygens et al., 2011) that have relatively thick and rigid cell

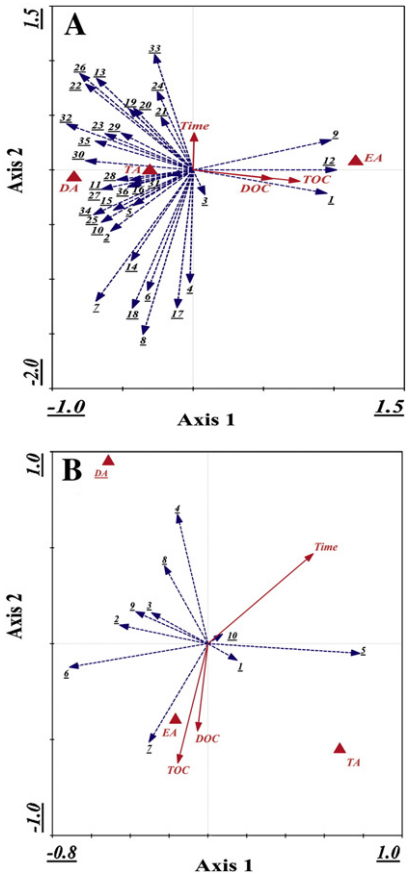

Fig. 7. The DGGE band data redundancy analysis (RDA) for bacterial (A) and fungal (B) community structure. Environmental parameters are indicated by triangles (i.e., nominal variables are designated by EA, TA, or DA for erosional, transitional, or depositional area) or solid lines with filled arrows, while species parameters are shown using dashed lines with filled arrows. Each species parameter indicated by a number represents the total rDNA gene relative abundance of this species.

walls and can produce compatible solutes to enhance their osmoregulatory capabilities (Schimel et al., 2007). As a result, these groups' resistance to D/R helps to stabilize the overall fungal community structure after rainfall. In contrast, many bacterial species protected by soil aggregates become dormant rather than extinct under soil drying stress (Grayston et al., 2001). After rewetting, increased carbon availability (Steenwerth et al., 2005) and favorable hydrothermal conditions may arouse these groups and increase their populations to levels that can be measured by DGGE. However, significant changes may not occur at the overall microbial community level rather than at a certain species scale, which is consistent with Chowdhury et al. (2011), whose conclusions were based on total microbial PLFA abundance analysis.

4.2. Effects of site erosional or depositional characteristics on microbial response to rewetting

We detected intersite substantial variations in bacterial and fungal abundances as well as in community structures after rewetting. Analysis of microbial gene properties during the 180-h experiment showed that EA had higher fungal and bacterial populations than DA, possibly because the residue stacking practice at the top position of the sloping cropland had raised surface soil carbon content (Lal, 2004). The SOC and DOC that could trigger bacterial growth were detected at higher levels in EA than in DA. However, the bacterial populations' response to rewetting in EA showed similar patterns as that in DA, not only within the initial 24 h, but also throughout the entire experiment. Some researchers insisted that microbial populations' response to environmental stress is strongly regulated by soil properties (Kennedy and Papendick, 1995) and that the soil's capacity to protect microorganisms is directly and/or indirectly (i.e. through physical protection by aggregates) related to the reactive properties of clays (Six et al., 2006). Soil erosion, which strongly governs soil physical properties and surface characteristics, will create a severe environment for microorganisms in EA relative to DA by disruption of soil aggregates (Polyakov and Lal, 2008), and selective out-migration of labile carbon as well as fine clay particles.

Fungal populations were resistant to rewetting in EA, but decreased significantly after rewetting in TA and especially in DA. This result concurs with Six et al. (2006) who suggested that the presence of surface residues favored fungal growth because fungi, unlike bacteria, can bridge the soil–residue interface and use the spatially separated carbon and nitrogen resources by translocating soil inorganic nitrogen into carbon-rich surface residues. Meanwhile, a high proportion of fine clay components in EA, because of selective in-migration from erosional sites (Schiettecatte et al., 2008a,b), may increase the total water-holding capacity (Lund, 1959), which contributes to low soil matrix potential and accelerates death/lysis of the unprotected fungal cells. These differences or similarities in bacterial and fungal responses to rewetting between slope positions probably are influenced not only by the amount of carbon released into soil solution through residue covering and stacking, but also by the soil properties characterized by historical erosion.

Site erosion or deposit characteristics can also strongly influence microbial community structure after rewetting, with bacterial and fungal species typically prevailing in a legume-dominated and nutrient-rich depositional area. The DGGE analysis showed that, after rewetting, bacterial diversity increased instantly in TA and DA but not in EA. These results could be mainly explained in two ways. First, the different carbon distribution patterns at the three slope positions may be an important reason. Because of selective migration and deposition by erosion, TA and DA compared to EA might have high abundant substrates with different qualities (Wang et al., 2010), which could benefit a series of bacteria-functional communities. Second, efficient aggregation in DA (Tang et al., 2010) can protect bacterial diversity more effectively. Many bacterial species could survive during an overdrying period (Huygens et al., 2011), so their proliferation and growth will be enhanced once the soils were rewetted (Griffiths et al., 2003). Based on such extrapolation, the bacterial community structure in DA showed higher level resistance to rewetting than in EA or TA.

Because of rewetting, fungal diversity in EA gradually recovered from drying stress, but it was the opposite in TA. As bacteria, community structure of fungi in DA soils was more resistant to rewetting. These results may be consistent with Killham (1994), who suggested that micropores, which were richer in the depositional area (Martinez-Mena et al., 1998) resulting from the high content of clay fractions, were not conducive to the growth of fungi because of their larger size than bacteria. Nevertheless, this dense soil structure can also provide refuge for existing fungi against the attack from larger predators that are typically unable to contact with fungi through smaller pores (Six et al., 2006).

4.3. Relationship between soil microbial and carbon dynamics responses to rewetting

As indicated previously, fungal and bacterial abundance varied substantially between sites. However, only bacterial populations were involved in the carbon dynamics in our soils, as evidenced by a significant negative correlation between bacterial abundance and DOC in EA and TA soils from 0 to 60 h. Previous study found a remarkable pulse of CO_2 (i.e., Birch effect) produced by rewetting a dry soil (Birch and Friend, 1956), which is conducted by soil microorganisms and may be considered as an important depletion of soil carbon pools, especially labile carbon pools (including intracellular osmolytes, exposed SOC, and lysed cells) (Gordon et al., 2008). Therefore, we conclude

that the increase of bacterial populations should be an important reason in explaining the DOC reduction in EA and TA soils after rewetting. Moreover, soils' ability to retain nutrients also has significant influence on DOC dynamics, as Gordon et al. (2008) detected that DOC leaching after D/R was greatest from improved grassland soil that had a lower microbial biomass than unimproved grassland soil. This may partially explain why DOC was reduced in DA where the lowest microbial populations were observed, but no significant correlation with bacterial populations was found in EA or TA. From this point of view, eroded carbon deposition in DA may benefit carbon sequestration, especially in the hilly red soil region in south China with frequent and high intensity D/R during summer.

Our results suggest that the effects of site erosion or deposit characteristics on microbial community structure in response to rewetting could be related to soil carbon distribution. These results are consistent with Steenwerth et al. (2005), who suggested that rewetting response patterns in microbial community structure may be controlled by soil carbon availability. However, variations in bacterial community structure cannot be significantly explained by the carbon data set alone, but collaboratively by carbon data sets and site factors (i.e., the nominal variable in this study). This indicates that the carbon dynamics at the slope scale did not directly shape the bacterial community structure because of the spatial heterogeneity in erosion or deposit characteristics within the sloping cropland. In other words, the slope erosion or deposit characteristics can strongly influence the interaction between bacterial community structure and soil carbon distribution after rewetting. The apparent detection may be explained by the fact that distinct soil texture, structure, and nutrient conditions, which could be directly traceable to the migration and enrichment of sediment as well as soil carbon with different qualities during erosion, may favor a series of functional strains at different positions of the sloping cropland. As a result, different bacterial community structures and carbon turnover patterns are observed in different areas within the sloping land. Unlike in bacteria, the carbon data set solely explains 21.9% of the variation in fungal community structure, which suggests that fungal community structure may substantially influence or be influenced by soil carbon after rewetting.

5. Conclusions

The results of this study show that rewetting and site erosion or deposit characteristics had pronounced effects on microbial community composition and on soil carbon processes in the investigated sloping cropland. Greater microbial abundance was observed in samples from EA than from TA or DA following rewetting of dried soil. Fungal abundance was found to be more dynamic than bacterial abundance throughout the experimental period in response to rewetting stress. However, under rewetting conditions, observed variations in bacterial and fungal abundances did not significantly correlate with the dynamics of soil carbon pools at the site scale through the experiment. The results suggest that the responses of microbial growth and reproduction, as well as the efficiency of carbon utilization to rewetting, are dependent of site erosion or deposit characteristics. Levels of microbial community structure responding to rewetting stress varied widely between sites as well as functional groups. Bacterial species diversity increased immediately after rewetting at the middle and lower positions of the slope, especially in DA; while no similar response was detected in EA. Fungal community structure was found less sensitive to rewetting than bacterial, and this measure was rather dynamic in EA while obstinate in DA. Together with site variables, the carbon data set significantly influenced the variations in bacterial or fungal community structure after rewetting. Hence, we conclude that site erosion or deposit characteristics may affect the D/R susceptibility of soil biogeochemical carbon cycles by inducing shifts in functional microbial communities with differing responses to rewetting.

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