

Soil erosion-related dynamics of soil bacterial communities and microbial respiration



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ABSTRACT

Soil erosion can dramatically change physicochemical soil properties, but little is known about the responses of bacterial communities and microbial respiration to soil erosion. In this study, three sites (upslope, mid-slope and downslope) with different erosional and depositional characteristics were selected along three transects of abandoned land in the Qiaozhi watershed of the Chinese Loess Plateau to evaluate the impacts of soil erosion on bacterial communities and microbial respiration. Samples of the topsoil (0–10 cm) and subsoil (10–20 cm), classified as Calcic Cambisols, were collected from these sites. The results showed that lower bacterial abundance was observed in the topsoil of the downslope site (7.58×10^8 copies g^{-1} soil) relative to the upslope (9.32×10^8 copies g^{-1} soil) and mid-slope (8.70×10^8 copies g^{-1} soil) sites. However, no obvious change ($P > 0.05$) in the bacterial Shannon index and community composition was observed among the sites. Runoff-induced erosion and migration of sediment homogenized the bacterial communities along the eroded slopes. Soil microbial respiration in the topsoil of the downslope site (19.02 ± 0.25 mg CO_2-C kg^{-1} soil d^{-1}) was significantly ($P < 0.05$) higher than that of the upslope (15.12 ± 1.07 mg CO_2-C kg^{-1} soil d^{-1}) and mid-slope (17.75 ± 0.73 mg CO_2-C kg^{-1} soil d^{-1}) sites, indicating that the deposition of sediment and associated organic matter significantly increased the soil microbial respiration. Multiple stepwise regression analyses showed that available nitrogen was the main explanatory factor for the variation in soil microbial respiration in both the topsoil (60.2%, $P = 0.009$) and subsoil (80.3%, $P = 0.002$). Compared to the bacterial properties, the labile organic matter contributed more to the variation. Our work suggested that soil microbial respiration was primarily modulated by the quality of the organic matter.

1. Introduction

Soil erosion represents one of the main driving forces of soil carbon (C) dynamics (Li et al., 2016), and has elicited tremendous concern because it directly and indirectly contributes to the global C cycle (Park et al., 2014). The erosion process not only affects the spatial distribution of soil organic carbon (SOC) within a landscape but also influences the exchange of C between the soil and the atmosphere (Van Hemelryck et al., 2011). Over the past decade, the topic of the net impact of soil erosion on the global C cycle has been widely debated (Lal, 2005). On one hand, Lal and colleagues (Lal, 2005; Lal and Pimentel, 2008) declared that soil erosion is a source of atmospheric CO_2 . On the other

hand, Van Oost and other authors (Smith et al., 2005; Van Oost et al., 2008) argued that approximately 1 Gt C yr^{-1} might be sequestered through burial of SOC in the depositional environment.

To clarify the direction and magnitude of erosion-induced changes in the global C balance, the impact of soil erosion on the C dynamic has been widely investigated (Nie et al., 2014; Van Hemelryck et al., 2011). For example, Novara et al. (2016), through simulations, indicated that the transport of sediments along an eroded slope increases SOC mineralization by 43%. Based on indoor incubation experiment, Wei et al. (2016) reported that the CO_2 emission rate from the coarse aggregate fraction in a depositional site is significantly greater than that from the eroded site. Despite the fact that soil microorganisms represent a major

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component of the terrestrial biosphere, erosion-induced changes in soil microbial communities and the extent to which these changes are related to SOC dynamics have always been disregarded.

Soil microorganisms are sensitive to soil disturbances and play crucial roles in soil ecosystem functions by regulating the cycling of nutrient elements and the decomposition of organic matter (Hou et al., 2014). Most researchers consider the erosion process has a negative impact on microbial properties due to the reduction in soil nutrients, and indicate the mineralization of organic matter is mainly controlled by microbial community (Wei et al., 2016). In the study by Cleveland et al. (2014) and Xiao et al. (2017), the variation in soil microbial respiration was largely explained by the availability of labile organic matter. **A systematic understanding of the relationships between microbial respiration and abiotic and biotic soil properties remains lacking** due to the complicated interactions of physicochemical soil properties (e.g., pH, moisture and nutrient content), microbial community and respiration. Further understanding the responses of microorganisms to soil erosion and the links to SOC mineralization is very important for clarifying the mechanism governing soil C cycling. The goals of this study are to (i) investigate the response pattern of a bacterial community to soil erosion; (ii) explore the differences in soil microbial respiration between erosional and depositional sites; (iii) further evaluate the relationships between soil microbial respiration and abiotic and biotic soil properties.

Previous studies that focused on different land use types and vegetation patterns noted that an increase in soil nutrients was beneficial to the growth of soil microbes (Quideau et al., 2013; Six et al., 2006). Thus, in this study, our first hypothesis (H1) was that the bacterial abundance and diversity at the depositional site would be higher than the other sites due to the greater soil nutrient availability. In addition, our second hypothesis (H2) was that the deposition of sediments and associated organic matter resulted in an increase in the soil microbial respiration. To test our hypotheses, high-throughput sequencing was applied to intuitively discern the changes in the soil bacterial community. Furthermore, the radionuclide cesium-137 (^{137}Cs) was used to estimate the rates of soil erosion and deposition.

2. Materials and methods

2.1. Experimental sites

The study was located in the Qiaozhi watershed (coordinates 34°36'–34°37'N, 105°42'–105°43'E) in the hilly-gully region of the Loess Plateau, situated in the vicinity of Tianshui, Gansu Province, China (Fig. 1). The climate is semi-arid, with a mean annual precipitation of 496–628 mm and a mean annual temperature of 10.7 °C. The main soil type is black cinnamonic soil (Calcic Cambisol, FAO), which is silty in texture (9% sand, 71% silt and 20% clay) and weakly resistant to erosion. Three transects were selected on a southern slope of the watershed. The transects were close to each other, with the distances between any two transects varying from 0.5 to 1 km. Along the slope, three sites (an upslope site, UP; mid-slope site, MP; and a downslope site, DP) were selected for each of the three transects at equal intervals of 20 m (Fig. 2). The slope gradient at the UP, MP and DP sites were $9.60 \pm 1.21^\circ$, $11.53 \pm 2.37^\circ$, $5.65 \pm 1.10^\circ$, respectively. The land type of the three transects was abandoned land. The main crop grown on the land prior to abandonment was maize (*Zea mays* L.), and the dominated plants after 11 years of natural succession were *Heteropappus altaicus* and *Artemisia capillaries*.

2.2. Soil sampling and treatment

A 20 m × 20 m sampling plot was selected at each site. Three quadrats were randomly selected in each plot. Each quadrat had dimensions of 1 m × 1 m, and samples from each quadrat were collected using a 5-cm-diameter corer. Before collecting soil samples, the litter

layer of the topsoil (approximately 1 cm) was removed. For the topsoil (0–10 cm) and subsoil (10–20 cm), nine soil core samples were collected within each quadrat and then mixed together. Additionally, to calculate soil erosion and deposition rates, soil samples at 0–30 cm depths were also collected at each quadrat. Thus, a total of 54 soil samples (3 transects × 3 sites × 2 depths × 3 quadrats) and 27 ^{137}Cs samples (3 transects × 3 sites × 3 quadrats) were collected in May-2016. Each soil sample was divided into two subsamples: one was sieved (2 mm) and stored immediately at -70°C for the analysis of microbial properties; the other was air-dried for the determination of physicochemical soil properties. The ^{137}Cs samples were air-dried for the estimation of the ^{137}Cs inventory.

2.3. Laboratory analyses

2.3.1. Measurement of physicochemical soil properties

Air-dried soil samples were crushed with a wooden mallet and passed through a 2-mm sieve. Soil pH was determined with a digital pH meter (Woonsocket, RI, USA) using a soil-to-water ratio of 1:2.5 (w/v). Soil bulk density (BD) was analyzed using the cutting ring method, and the distribution of soil particle sizes was determined using the pipette method. Subsamples passed through a 1-mm sieve were used in the analysis of available nitrogen (N) via the alkali N-proliferation method (Duan et al., 2016). Subsamples passed through a 0.25-mm sieve were used in the analysis of SOC and total nitrogen (TN). The SOC was determined using the dichromate oxidation method (Walkley and Black, 1934); and TN was measured using the Kjeldahl (1883) method. Dissolved organic carbon (DOC) was measured as described by Li et al. (2015). The chloroform-fumigation extraction method was used to determine microbial biomass carbon (MBC) (Vance et al., 1987). The basic physicochemical soil properties at different sites and depths are presented in Table 1.

2.3.2. Measurement of ^{137}Cs inventory

Air-dried soil samples (0–30 cm) were passed through a 1-mm sieve. The fine fraction (under 1 mm) was used for the ^{137}Cs analysis. The ^{137}Cs content (Bq kg^{-1}) was determined using a hyperpure Li-drifted Ge detector coupled to a DSPEC multichannel gamma-ray spectrophotometer (GMX50, PerkinElmer, USA). The detector had a 2.17 keV (^{60}Co) energy resolution and was calibrated using standard certified samples purchased from the China Institute of Atomic Energy. Gamma emissions from ^{137}Cs at 661.6 keV were counted for 28,800 s, yielding results with an analytical precision of $\pm 5\%$.

2.3.3. Determination of bacterial communities

The composite sample for each site and depth along the transects (a total of 18 composite samples, i.e., 3 transects × 3 sites × 2 depths) was used in the analysis of the bacterial community via Illumina MiSeq sequencing. Soil DNA was extracted with a Powersoil[®] DNA Isolation kit (Omega Bio-Tek, USA). The bacterial 16S ribosomal RNA gene was amplified by polymerase chain reaction (PCR) using the primers 338F (5'-barcode- ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3'). The PCR reaction was performed in a 20- μl reaction mixture containing 1 μl of template DNA (10 ng μl^{-1}), 2 μl of 2.5 mM dNTPs, 4 μl of 5 × FastPfu Buffer, 0.8 μl of each primer (5 μM) and 0.4 μl of FastPfu Polymerase (Sun et al., 2015). The PCR conditions were as follows: denaturation at 95 °C for 3 min, followed by 27 cycles at 95 °C for 30 s, 55 °C for 30 s, 72 °C for 45 s, and final extension at 72 °C for 10 min. The purified PCR amplicons were pooled at equimolar ratios and paired-end sequenced (2 × 250) on the Illumina MiSeq PE300 platform (Illumina Corporation, USA). Clustering of the screened sequences into operational taxonomic units (OTUs) was performed using UPARSE (version 7.1) at a 97% similarity threshold. Relative abundance (%) was defined as the number of OTUs affiliated with the same microbial taxa divided by the total OTUs number. Additionally, the Shannon index was calculated as the description of

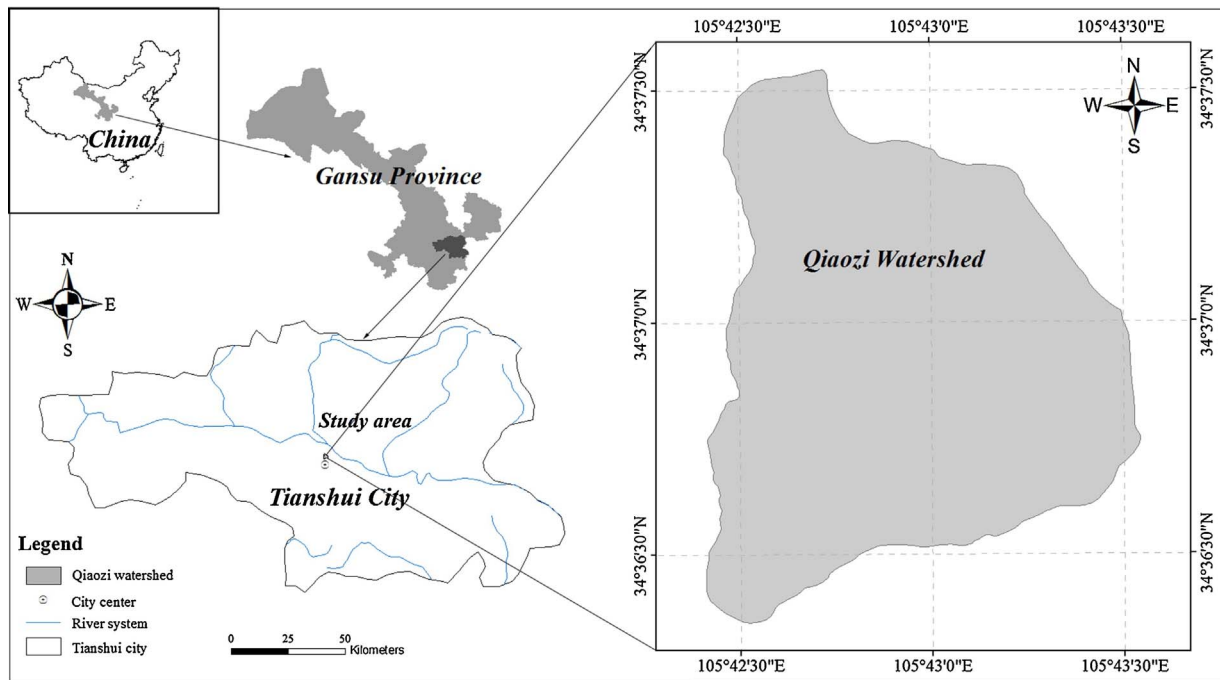


Fig 1. The location of study area.

Huang et al. (2013).

2.3.4. Quantification of bacterial abundance

The bacterial abundance was determined by real-time quantitative PCR (qPCR) of the 16S rRNA gene with the following primer pairs: 338F (5'-ACTCCTACGGGAGGCGAGCAG-3') and 518R (5'-ATTACCGGGGCTGCTGG-3') (Huang et al., 2013). Amplifications were performed in a 20- μ l reaction mixture containing 2 μ l of purified-DNA template, 1 μ l of each primer (10 μ M) and 16 μ l of 2 \times Real SYBR Mixture. The PCR conditions were as follows: initial denaturation at 95 $^{\circ}$ C for 10 min, followed by 40 cycles at 95 $^{\circ}$ C for 15 s, 53 $^{\circ}$ C for 15 s, and 72 $^{\circ}$ C for 30 s (Tian et al., 2015). To evaluate the amplification specificity, the PCR products were subjected to melt curve analyses. The standard curve for qPCR was determined using ten-fold serial dilutions of cloned genes. The order of magnitude was 1.0×10^3 – 1.0×10^7 copies of template.

2.3.5. Calculation of soil erosion and deposition rates

The soil erosion and deposition rates were calculated using the ^{137}Cs

inventory variance between the sampling sites and the reference site. Sampling sites that had lower ^{137}Cs inventories than the reference value were considered to be erosional, and those with greater ^{137}Cs inventories than the reference value were considered to be depositional (Nie et al., 2010). The net erosion rate was calculated using the cultivated land and modified mass balance model proposed by Zhang et al. (1990):

$$X_n = X_0(1 - \Delta h/H)^{n-1963} \tag{1}$$

where X_n is the inventory of ^{137}Cs at the sampling site (Bq m^{-2}), X_0 is the ^{137}Cs reference inventory (Bq m^{-2}), H is the depth of the plow layer (cm), Δh is the depth of soil loss (cm), and n is the year of sampling. The annual average erosion rate was calculated as follows:

$$M = 10000 \cdot \Delta h \cdot D \tag{2}$$

where M is the annual average erosion rate ($\text{t km}^{-2} \text{yr}^{-1}$) and D is the bulk soil density (g cm^{-3}). The soil deposition rate was calculated using the equation proposed by Lowrance et al. (1988):

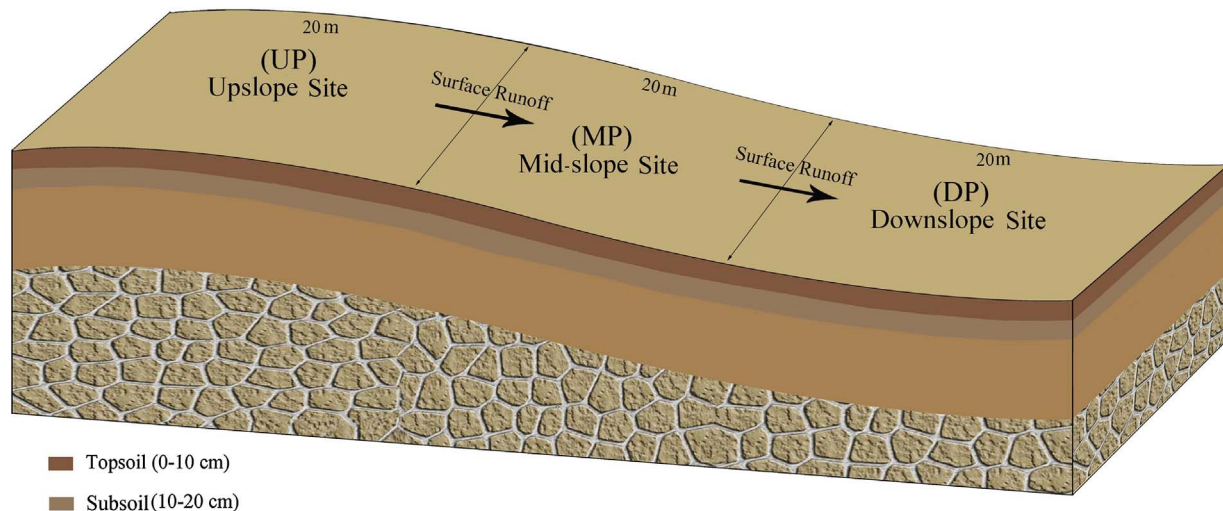


Fig. 2. Sketch of the study sites along the slope.

Table 1
Soil physicochemical properties at different sites and depths of the eroded slope.

Soil depths (cm)	Sites	Moisture (%)	pH	BD (g cm ⁻³)	Sand (%)	Silt (%)	Clay (%)
0–10	UP	11.4 (0.4) ^a	7.74 (0.02) ^b	1.22 (0.03) ^a	8.6 (1.1) ^a	69.9 (2.0) ^a	21.5 (0.8) ^a
	MP	11.0 (1.0) ^a	7.64 (0.06) ^c	1.13 (0.03) ^b	8.6 (0.3) ^a	71.2 (0.5) ^a	20.2 (0.8) ^{ab}
	DP	11.7 (0.7) ^a	8.20 (0.03) ^a	1.18 (0.05) ^{ab}	9.2 (3.3) ^a	71.0 (2.1) ^a	19.8 (1.2) ^b
10–20	UP	10.7 (0.5) ^a	7.79 (0.04) ^b	1.24 (0.03) ^a	7.2 (0.8) ^a	68.8 (0.9) ^a	24.0 (0.1) ^a
	MP	10.9 (0.2) ^a	7.87 (0.06) ^b	1.25 (0.11) ^a	7.8 (1.1) ^a	70.4 (1.4) ^a	21.8 (0.9) ^b
	DP	11.5 (0.5) ^a	8.31 (0.20) ^a	1.26 (0.08) ^a	8.1 (2.9) ^a	69.7 (2.3) ^a	22.2 (1.0) ^{ab}

UP: upslope site; MP: mid-slope site; DP: downslope site; BD: bulk density.

* Numbers in brackets are the standard errors of the means. For each soil depth, values labeled with the same letter are not significantly different at $P < 0.05$.

$$S = \frac{C - Z}{(N - 1954)W_d} \times 1000 \quad (3)$$

where S is the annual average soil deposition rate ($\text{t km}^{-2} \text{ yr}^{-1}$), C is the ^{137}Cs inventory at the deposition site (Bq m^{-2}), Z is the ^{137}Cs reference inventory, W_d is the weight content of ^{137}Cs at the deposition site (Bq kg^{-1}), and N is the year of sampling.

2.3.6. Soil incubation experiment

Fresh soils adjusted to 60% of their water holding capacity were incubated at 25 °C for 7 d to stabilize the microbial activity before measurement (Wang et al., 2014). To perform the incubation, 50 g of pre-incubated soils was placed in a 1000-ml glass jar. A plastic bottle containing 20 ml of 0.1 M NaOH solution was placed in each glass jar to trap evolved CO_2 from the soil. Three additional jars, each containing a bottle with 20 ml of NaOH solution (0.1 mol L^{-1}), were used as controls to calculate the CO_2 trapped from the air. All the jars were incubated in the dark at 25 °C for 40 d. Bottles with NaOH solution containing trapped CO_2 were collected after 1, 4, 7, 14, 21, 28 and 40 d. The jars were ventilated for 0.5 h after the collection of the NaOH samples. The amount of CO_2 evolved from the incubated soil was determined via titration against 0.5 M HCl (Rabbi et al., 2014).

2.4. Statistical analysis

To generate a normal distribution, the bacterial abundance was \log_{10} -transformed. One-way ANOVA, followed by a least-squares difference (LSD) test (95% confidence level), was performed to test for differences among the means. Multiple stepwise regression analysis was used to analyze the contributions of abiotic and biotic soil properties to the variations in microbial respiration observed in both the topsoil and the subsoil. In total, 9 physicochemical soil properties (SOC, TN, available N, DOC, MBC, sand, silt, clay and pH) and 2 biotic variables (bacterial abundance and Shannon index) were selected. All explanatory (biotic and abiotic) variables were checked for collinearity, and the variance inflation factors (VIFs) were < 3 for all test variables. All statistical analyses were performed using the software program SPSS ver. 19.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Erosion-induced changes in physicochemical soil properties

A comparison of the soil ^{137}Cs inventories to the reference value ($1400.70 \pm 199.80 \text{ Bq m}^{-2}$) confirmed that UP and MP sites were primarily erosional, with ^{137}Cs inventories below the reference value. In contrast, the DP site with an elevated ^{137}Cs inventory ($1502.82 \pm 63.90 \text{ Bq m}^{-2}$) was predominantly depositional (Table 2). The erosion rates in the UP and MP sites were $3148.22 \pm 84.70 \text{ t km}^{-2} \text{ yr}^{-1}$ and $2011.39 \pm 230.00 \text{ t km}^{-2} \text{ yr}^{-1}$, respectively. The deposition rate for the DP site was $404.45 \pm 156.40 \text{ t km}^{-2} \text{ yr}^{-1}$ (Table 2). The SOC and TN contents in the topsoil of the DP site (11.97 mg g^{-1} and 6.73 mg g^{-1} ,

respectively) were significantly ($P < 0.05$) greater than those in the UP and MP sites (Fig. 3a, 3b), while no significant differences ($P < 0.05$) in the DOC content of the topsoil among the UP, MP and DP sites were observed (Fig. 3c). The MBC was greatest in the topsoil of the MP site (0.41 mg g^{-1}) and was 1.29 and 1.10 times higher than the contents in the UP and DP sites, respectively (Fig. 3d). Available N was significantly ($P < 0.05$) greater in the topsoil of the MP and DP sites than that of the UP site (Fig. 3e). No significant difference ($P < 0.05$) existed among the C:N values of the UP, MP and DP sites (Fig. 3f). In addition, the SOC, TN, DOC, MBC and available N contents in the topsoil were higher than those in the subsoil.

3.2. Changes in bacterial abundance and community composition

The bacterial abundance ranged from 5.65×10^8 to 9.32×10^8 copies g^{-1} soil. Statistical analysis showed that the bacterial abundance in the topsoil of the UP site was significantly greater ($P < 0.05$) than that in the DP site. There was no obvious ($P > 0.05$) change in the Shannon index among the UP, MP and DP sites (Fig. 4). The dominant bacterial phyla were *Proteobacteria*, *Actinobacteria*, *Acidobacteria* and *Chloroflexi*, which in total accounted for 65.3% of the OTUs. *Proteobacteria* accounted for 24.9% of the total OTUs and was the most predominant bacterial phylum. No obvious changes occurred in the bacterial community composition among the UP, MP and DP sites (Fig. 5). The dominant phylum was analyzed further. Among the *Proteobacteria*, *Alpha*-, *Beta*-, *Gamma*-, and *Delta*-*proteobacteria* were found at all sites. The *Delta*-*proteobacteria* dominated this phylum and represented 9.5% of all populations. *Alpha*-, *Beta*-, and *Gamma*-*proteobacteria* comprised 6.8%, 3.4% and 5.0% of the total populations, respectively. No obvious ($P > 0.05$) changes at the class level of *Proteobacteria* were observed among the sites (Fig. 6). At the order level, *Myxococcales* dominated the *Delta*-*proteobacteria* populations. Except for *Oligoflexales*, no obvious ($P > 0.05$) changes at the order level of *Delta*-*proteobacteria* were observed among the sites (Fig. S1 in the online version at DOI: <http://dx.doi.org/10.1016/j.apsoil.2017.06.018>).

3.3. Changes in soil microbial respiration

The cumulative $\text{CO}_2\text{-C}$ emitted from the study sites during the 40-d incubation is shown in Fig. 7. The highest CO_2 emission rate was observed at incubation times of 14–28 d. The soil microbial respiration in the topsoil of the DP site ($19.02 \pm 0.25 \text{ mg CO}_2\text{-C kg}^{-1} \text{ soil d}^{-1}$) was significantly ($P < 0.05$) higher than that in the UP and MP sites. Furthermore, relative to the topsoil, a lower microbial respiration was observed in the subsoil (Table 3). The C mineralization ratio (emitted CO_2 divided by the SOC) ranged from 0.060 to $0.091 \text{ g CO}_2\text{-C g}^{-1} \text{ SOC}$, and in the topsoil of the DP site, it was significantly ($P < 0.05$) lower than that in the UP and MP sites. The metabolic quotient ($q\text{CO}_2$, the ratio of soil microbial respiration to MBC) ranged from 1.92 to $3.01 \text{ mg CO}_2\text{-C g}^{-1} \text{ MBC h}^{-1}$ (Table 3). There was no significant ($P > 0.05$) difference in $q\text{CO}_2$ among the UP, MP and DP sites.

Table 2
Caesium-137 (¹³⁷Cs) levels as well as the estimated soil erosion and deposition rates in different sites.

Sites	Status	¹³⁷ Cs mass activities (Bq kg ⁻¹)	¹³⁷ Cs inventories ^a (Bq m ⁻²)	Erosion or deposition thickness (cm yr ⁻¹)	Erosion or deposition rate (t km ⁻² yr ⁻¹)
UP	Eroding	1.96 (0.15) ^b	711.48 (54.45)	0.29 (0.01)	3148.22 (84.70)
MP	Eroding	2.55 (0.23)	879.75 (79.35)	0.18 (0.02)	2011.39 (230.00)
DP	Deposition	4.14 (0.21)	1502.82 (63.90)	0.03 (0.01)	404.45 (156.40)

UP: upslope site; MP: mid-slope site; DP: downslope site.

^a¹³⁷Cs reference inventory is 1400.70 ± 199.80 Bq m⁻².

^b Numbers in brackets are the standard errors of the means.

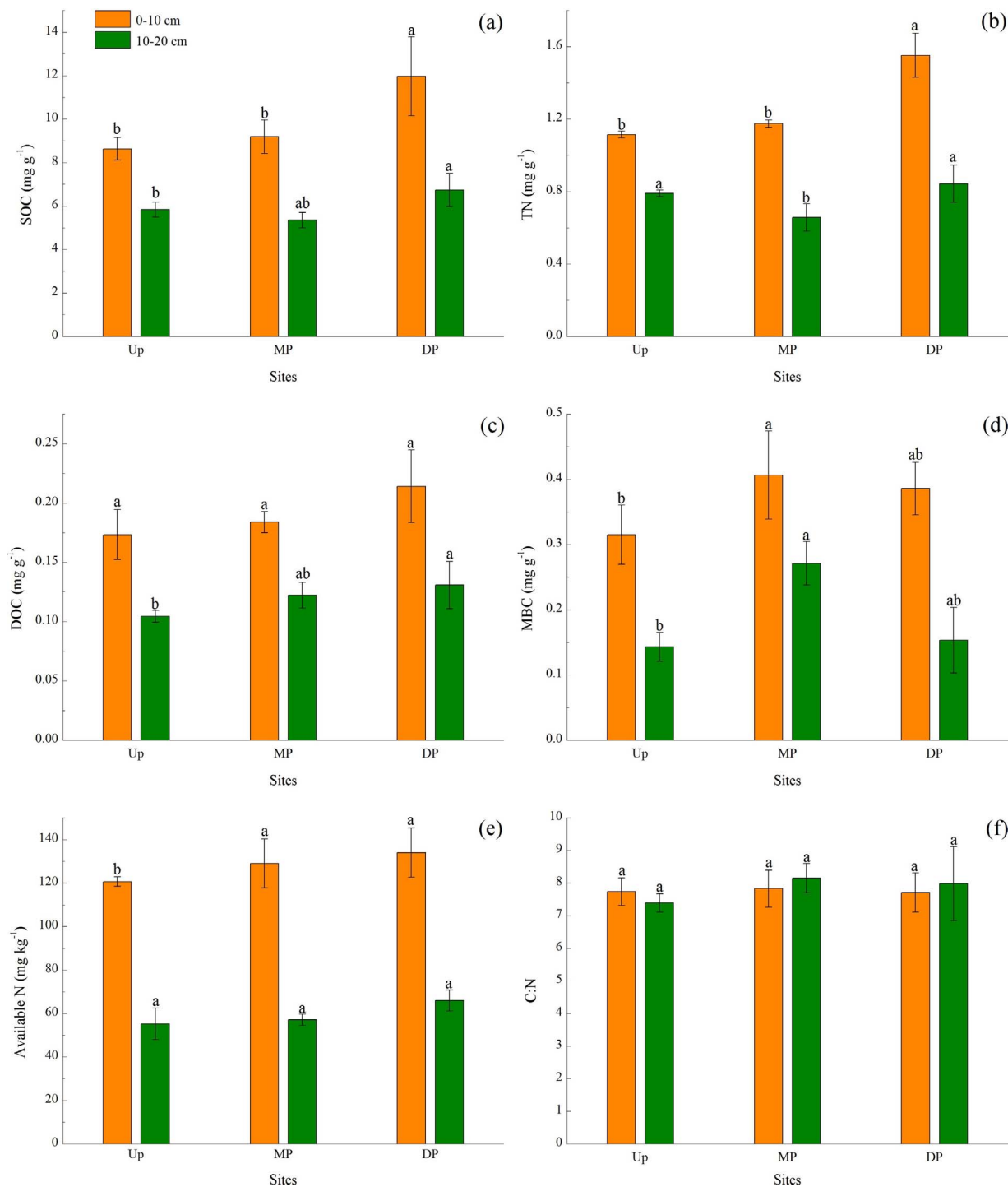


Fig. 3. The concentrations of (a) soil organic carbon (SOC), (b) total nitrogen (TN), (c) dissolved organic carbon (DOC), (d) microbial biomass carbon (MBC), (e) available N and (f) the ratio of carbon and nitrogen (C:N) at different sites (UP: upslope site; MP: mid-slope site; DP: downslope site) and depths. The error bars represent the standard errors of the means. For each soil depth, the plots labeled with the same letter are not significantly different at $P < 0.05$.

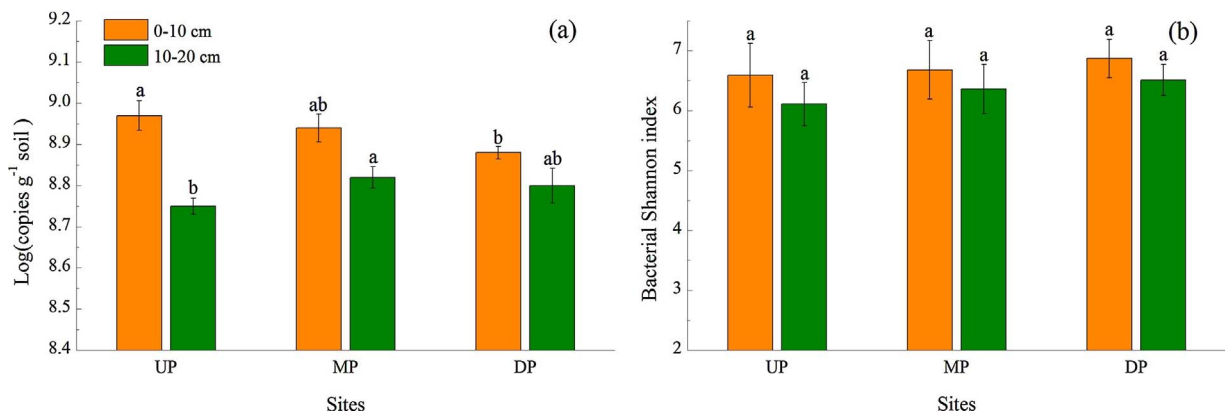


Fig. 4. Bacterial abundance (a) and Shannon index (b) at different sites and depths. For each soil depth, the plots labeled with the same letter are not significantly different at $P < 0.05$. (UP10: 0–10 cm soil of the upslope site; MP10: 0–10 cm soil of the mid-slope site; DP10: 0–10 cm soil of the downslope site; UP20: 10–20 cm soil of the upslope site; MP20: 10–20 cm soil of the mid-slope site; DP20: 10–20 cm soil of the downslope site).

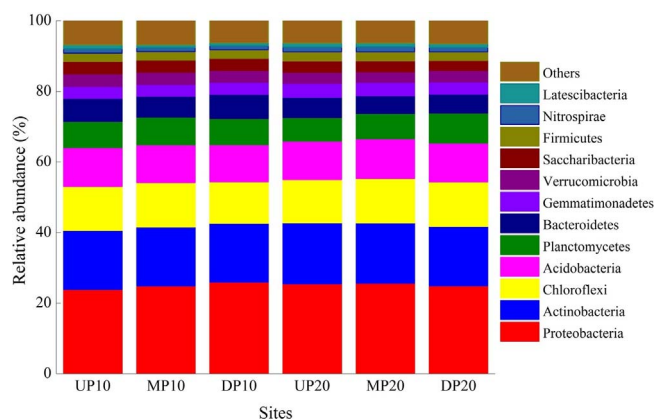


Fig. 5. Relative abundance of soil bacterial communities at the phylum level at different sites and depths.

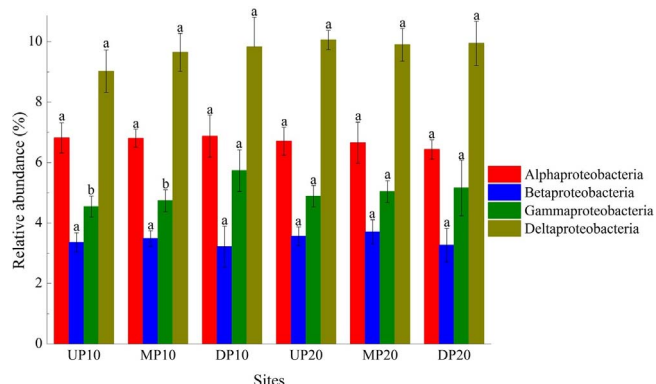


Fig. 6. Relative abundance of the soil *Proteobacteria* communities at the class level at different sites and depths. For each soil depth, the plots labeled with the same letter are not significantly different at $P < 0.05$.

3.4. Associations between soil microbial respiration and abiotic and biotic soil properties

A large proportion of the variance in soil microbial respiration was explained using multiple regression models with selected soil properties. At the 0–10 cm soil depth, 60.2% of the variance in the soil microbial respiration was explained by available N ($P = 0.009$). At the 10–20 cm soil depth, 94.6% of the variance in the soil microbial respiration was explained by the set of abiotic and biotic soil properties ($P < 0.01$). Available N, which explained up to 80.3% of the variation, was the main explanatory factor for soil microbial respiration

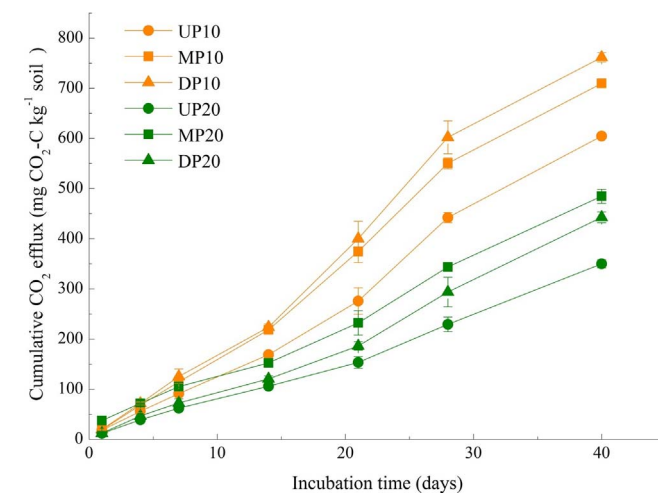


Fig. 7. Cumulative CO₂ efflux at different sites and depths. The vertical bars are standard deviations.

Table 3
Soil microbial respiration, C mineralization ratio and metabolic quotient at different sites and depths of the eroded slope.

Soil depths (cm)	Sites	Soil microbial respiration (mg CO ₂ -C kg ⁻¹ soil d ⁻¹)	C mineralization ratio (g CO ₂ -C g ⁻¹ SOC)	Metabolic quotient (mg CO ₂ -C g ⁻¹ MBC h ⁻¹)
0–10	UP	15.12 (1.07) ^c	0.070 (0.005) ^b	2.00 (0.36) ^a
	MP	17.75 (0.73) ^b	0.082 (0.003) ^a	1.92 (0.21) ^a
	DP	19.02 (0.25) ^a	0.064 (0.001) ^c	2.06 (0.09) ^a
10–20	UP	8.75 (1.06) ^b	0.060 (0.007) ^b	2.54 (0.28) ^a
	MP	12.12 (1.34) ^a	0.091 (0.010) ^a	2.85 (0.31) ^a
	DP	11.07 (1.59) ^a	0.066 (0.009) ^b	3.01 (0.49) ^a

UP: upslope site; MP: mid-slope site; DP: downslope site.

* Numbers in brackets are the standard errors of the means. For each soil depth, values labeled with the same letter are not significantly different at $P < 0.05$.

($P = 0.002$), and the bacterial Shannon index explained 14.3% of the variation ($P = 0.004$) (Table 4).

4. Discussion

Soil microorganisms are actively involved in soil biochemical processes, including organic matter decomposition, nutrient mineralization and cycling (Bowles et al., 2014). In this study, soil erosion and deposition estimation models based on the ¹³⁷Cs inventory were combined with soil bacterial community and microbial respiration

Table 4
Results of multiple stepwise regression analysis.

Dependent variables	Soil depths (cm)	Explaining variables	Coefficients	S.E.	t-value	P-value	Explained variability (%)
Soil microbial respiration	0–10	Constant	368.296	97.344	3.783	0.007	60.2
		Available N	6.101	1.686	3.618	0.009	
		Adjusted R ²		0.602			
	10–20	Constant	–1396.508	295.734	–4.722	0.003	80.3
		Available N	9.749	1.939	5.027	0.002	
		Shannon index	236.563	53.416	4.429	0.004	
		Adjusted R ²		0.946		14.3	

S.E.: standard error.

measurements to investigate the response of soil microbiological properties to soil erosion, and to evaluate the relationships between soil microbial respiration and abiotic and biotic soil properties in erosion-affected soil. The results showed that there was no significant difference in bacterial species diversity between the erosional and depositional sites, which was consistent with the findings of several similar studies (Huang et al., 2013; Li et al., 2015; Zhao et al., 2016). For example, Li et al. (2015) reported that no obvious change in microbial diversity was observed between erosional and depositional sites in an intact watershed. Huang et al. (2013) also indicated that the Shannon index of bacteria and fungi exhibited minimal changes during a rainfall simulation in a sloping farmland. This phenomenon might be related to the nonselective migration of microbial species due to runoff and sediment transport. Water-driven soil erosion is a natural hydrologic process. Soil particles inhabited by various microbial species are transported with the overland runoff, homogenizing the microbial species along the eroded slope (Huang et al., 2013).

Compared with the depositional site, the erosional sites were featured with higher bacterial abundances. Although the positive relationships between soil organic matter and microbial abundance has long been established for paddy and forest soil (Drenovsky et al., 2004; Park et al., 2014), no clear evidence existed for the coupled changes in soil nutrients and bacterial abundance due to disturbances related to soil erosion. Therefore, the results of this study indicated that soil nutrients might not be the primary influencing factor for the bacterial abundance in the eroded soil, although soil nutrient changes clearly had a strong influence on soil microbial properties. Thus, the first hypothesis (H1), i.e., that bacterial abundance and diversity at the depositional site should be higher due to the increase in soil nutrients, could not be supported. Unlike soil nutrients, changes in the pH of the soil have been shown to have marked impacts on microbial abundance (Drenovsky et al., 2004; Rousk et al., 2010). As described by Rousk et al. (2010), the optimal pH ranges for soil bacterial communities are in the region of 4–8, and soil bacterial abundance significantly decreases when the soil pH deviates from the optimal pH range. Therefore, the high soil pH (Table 1) in the topsoil of the depositional site might be the main factor accounting for the low bacterial abundance due to inhibition of the normal growth of soil bacteria.

The cloned sequences obtained from both erosional and depositional sites included various bacterial groups, such as *Proteobacteria*, *Actinobacteria*, *Acidobacteria* and *Chloroflexi* (Fig. 5). Our results showed that no obvious differences in bacterial community composition existed between the erosional and depositional sites. Based on the C mineralization potential and growth rate, soil bacteria can be classified into two ecological categories, copiotrophs and oligotrophs. Many soil *Proteobacteria*, such as *Alpha*- and *Gamma*-*proteobacteria*, are copiotrophic and abundant in nutrient-rich environments, whereas members of the phyla *Actinobacteria* and *Acidobacteria* are considered oligotrophs (Zhang et al., 2016a). However, compared with the erosional sites, higher abundances of *Alpha*- and *Gamma*-*proteobacteria* were not observed in the nutrient-rich depositional site (Fig. 6). This inconsistent result indicated that the microbial community composition of the eroded soil did not simply depend on the basic edaphic properties. The

microbial community composition might instead be closely related to runoff, the erosion-induced migration of sediment, and the disruption of soil aggregates, but this possibility required further investigation.

Soil microbial respiration, which originates from litter and organic matter decomposition, represents one of the most important routes of CO₂ flux from the soil surface to the atmosphere (Esch et al., 2016). Our results showed that the C mineralization ratios at the erosional sites were dramatically higher than those at the depositional site, indicating that the organic carbon stored in the eroded soils was vulnerable to microbial decomposition. The reduction effects of physical protection on SOC might be responsible for the high C mineralization ratios at the erosional sites. Severe soil erosion promotes the breakdown of soil aggregates and organic-mineral complexes and exposes previously encapsulated SOC to soil microorganisms, thereby increasing the mineralization potential of the SOC in the eroding landform (Li et al., 2017; Liu et al., 2017; Wei et al., 2016). In contrast, efficient aggregation at the depositional site provides effective protection for soil organic matter. The soil microbial respiration at the depositional site was significantly higher than that at the eroded sites ($P < 0.05$), although a high C mineralization ratio was observed at the erosional sites. This phenomenon might be related to the increase in the amount of organic matter at the depositional site. Soil microbial activity can be greatly increased by increasing the organic matter content (Lanza et al., 2016; Wang et al., 2014). For example, Wang et al. (2014) reported that leaf litter input could stimulate SOC mineralization. Zhang et al. (2016b) indicated that microbial respiration was positively correlated with NH₄⁺, MBC and SOC. The deposition of C-rich topsoil transported from the erosional sites dramatically increased the amount of soil organic matter at the depositional site, thereby stimulating soil microbial respiration. Thus, the second hypothesis (H2), i.e., that the deposition of sediments and associated organic matter increased soil microbial respiration, was verified. Furthermore, the results of the multiple stepwise regression analysis revealed that available N was the main explanatory factor for the variation in soil microbial respiration in both topsoil and subsoil. Compared to bacterial properties, a greater contribution of labile organic matter to the variation in soil microbial respiration was observed. This result indicated that the effects of changing microbial properties on soil microbial respiration were likely to be smaller than the potential effects of organic matter quality changes in response to soil erosion. This phenomenon was also observed in other studies (Calbrix et al., 2007; Cleveland et al., 2014). For example, Calbrix et al. (2007), using long-term laboratory incubation experiments, discovered that substrate amendments affected microbial respiration but did not significantly alter microbial biomass. In our study, high rates of microbial respiration were observed in the depositional soil with low bacterial abundance. Although limited microbial respiration would begin to occur at a specific minimum value of microbial biomass (Uchida et al., 2012), we did not appear to reach this minimum during our study. Our work noted that labile organic matter was the primary controlling factor for soil microbial respiration.

Relative to bacterial properties, a greater contribution of labile organic matter to the variation in soil microbial respiration was observed here. However, considering the importance of soil microorganisms in

soil C-cycling and the limitations of laboratory mineralization incubation experiments, further research is required to clearly elucidate the impacts of erosion-induced changes in abiotic and biotic soil factors on soil microbial respiration under the field conditions.

5. Conclusions

In this study, the responses of a bacterial community and microbial respiration to soil erosion were examined. Soil microbial respiration at the depositional site was significantly higher than that at the eroded sites, while no significant differences in bacterial species diversity and community composition were observed between the erosional and the depositional sites. Runoff and erosion-induced migration of sediment homogenized the bacterial community along the eroded slope, and the deposition of sediments and associated organic matter significantly enhanced microbial respiration at the depositional site. The results of the multiple stepwise regression analysis showed that available N was the main explanatory factor for the variation in soil microbial respiration. Compared to bacterial properties, a greater contribution of labile organic matter to the variation in soil microbial respiration was observed. Our work suggested that soil microbial respiration was primarily modulated by the quality of organic matter.

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