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Microbial Nonlinear Response to a Precipitation Gradient in the Northeastern Tibetan Plateau

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The response of soil microbes to global warming, especially their response to precipitation, remains poorly known. The Tibetan Plateau is very sensitive to climate change. In particular, the northeastern margin of the Tibetan Plateau is an interesting area to test the response of soil microbial communities to precipitation, as there is a distinct gradient in annual precipitation from east to west. We collected soil samples along a precipitation gradient in arid and semi-arid areas of the northeastern Tibetan Plateau. Phospholipid fatty acid (PLFA) technology was used to analyze the microbial community structure and total microbial biomass. With declining precipitation, bacterial biomass decreased significantly, whereas fungal biomass did not show an obvious trend; this result indicates that bacteria are more sensitive to mean annual precipitation (MAP). Overall, the biomass of Gram-negative (G⁻) bacteria represented up to 82% of the total bacterial biomass. In the high (260–394 mm yr⁻¹) MAP areas, bacterial biomass was mainly concentrated at the surface and decreased with increasing soil depth (0–40 cm). In contrast, in the low (36–260 mm yr⁻¹) MAP areas, bacterial biomass was mainly concentrated in the deep soils. The mean annual precipitation was strongly correlated with soil microbial communities in the 20–40-cm soil depth of this arid and semiarid region. The clustering of the microbial communities was significantly grouped according to the MAP gradient, revealing that MAP is a major driving force of microbial communities in this arid and semi-arid area. The decline in MAP led to a shift in the structure of the microbial community and an overall reduction in microbial biomass.

Keywords: arid and semiarid areas, mean annual precipitation, microbial community, PLFA

Introduction

The goal of biogeography is to reveal where organisms live, how abundant they are, and what environmental factors determine that abundance (Martiny et al. 2006). Plant community assembly and abundance at different spatial scales has been intensively investigated. Biogeographic patterns of plants are strongly dependent on geographical locations, site temperature, latitude and other climatic variables, and/or the extent of geographical isolation (Dequiedt et al. 2011; MacArthur and Wilson 2001; Martiny et al. 2006). The biogeographic patterns of macroorganisms are well documented and accepted, but the biogeographic patterns of microorganisms remain poorly understood.

Despite the key role of microbes in the carbon, nitrogen, phosphorous and sulfur biogeochemical cycles, few studies

have studied the distribution patterns of microbes on a local or regional scale, other than field plots. The investigation of the geographic distribution of macroorganisms has provided insights into the mechanisms that generate and maintain diversity in macroorganisms, e.g., speciation, extinction, dispersal and species interactions (Brown and Lomolino 1998), and may help to shed light on microbial processes. Microbial activities are often dependent on local environmental factors such as temperature, moisture, enzyme activity, and nutrient availability, all of which are likely to be affected by climate change. Climate change may have greater implications for crucial ecological processes, such as nutrient cycling, that rely on microbial activities.

The response of soil microorganisms to climate change may have a strong influence on ecosystem processes and represents a great uncertainty for ecosystem feedbacks to climate change (IPCC 2007a; IPCC 2007b). On one hand, microbes are the most diverse and abundant class of organisms on earth, comprising millions of species (Torsvik et al. 2002). On the other hand, the diversity of microbes in soil is critical to the maintenance of soil health because microbes are involved in many important soil functions such as carbon

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and nitrogen cycling, as well as organic-matter degradation (Ibekwe et al. 2002). Although soil microorganisms play critical roles in influencing many ecosystem functions, less is known about factors that influence microbial community structure at a large spatial scale.

It is known that the soil microbial community can be influenced by many factors, such as the mean annual precipitation (Bachar et al. 2010), soil moisture (Landesman and Dighton 2011), organic matter content (Hogberg et al. 2007), temperature (Wu et al. 2009), and pH (Rousk et al. 2010). Studies of how communities respond to precipitation gradients center on diversity patterns across a wide variety of taxonomic groups, including trees, birds, reptiles and insects (Dequiedt et al. 2011). More precisely, precipitation gradients, water availability and evapotranspiration have been shown to be the most essential factors influencing the distribution of regional plant communities (Kreft and Jetz 2007).

Spatial variation in mean annual precipitation could act as a primary factor that would weight ecosystem processes such as soil respiration (Raich and Potter 1995; Yuste et al. 2007), decomposition (Adair et al. 2008; Aerts 1997; Epstein et al. 2002), and plant productivity (Lauenroth and Sala 1992; Sala et al. 1988). This is especially true in arid and semi-arid areas, where the mean annual precipitation is a very important and limiting factor that affects soil moisture and soil microbial basal respiration (Wichern and Joergensen 2009). Soil microbial abundance is reduced when the mean annual precipitation is low (Bachar et al. 2010).

Soil moisture has been shown to influence the soil microbial community composition (Kieft et al. 1993; Lundquist et al. 1999; Schimel et al. 1999). Microbial biomass can rapidly respond to precipitation (Angel et al. 2010). In addition to the amount of precipitation, the period and intensity of the precipitation could also have a significant impact on soil microbial communities because microbial growth and activity is often dependent upon the diffusion of substrates through soil water (Clarholm and Rosswall 1980). Hackl et al. (2005) found that the microbial community PLFA pattern was strongly influenced by soil water. However, few studies have tested how a low precipitation gradient would impact the spatial distribution of the microbial community. There are various microbial communities in different geographic conditions; a good understanding of the potential changes in those microbial communities in response to precipitation gradients over a large region and the underlying mechanisms for those changes has scientific and economic merit, especially within the context of potential climate change.

Phospholipid fatty acids (PLFAs), parts of the microbial cell membrane, are very sensitive to environmental change (Frostegård et al. 2011). Phospholipid fatty acids are used as indicators of the microbial community structure because certain groups of microbes have different 'signatures' of fatty acids (Tunlid et al. 1989). Lovell et al. (1995) suggested that PLFAs were associated with changes in community structure, in particular in the relative proportion of bacteria to fungi. In comparison with pyrosequencing, microarrays, qPCR and clone libraries, the PLFA technique is widely used by ecologists, as PLFA shows an overview of the microbial

community by providing quantitative information on functional groups and environmental stresses (Frostegård et al. 2011). Thus, the PLFA technique was employed in this study.

The Tibetan plateau is very sensitive to climate change (Yao et al. 2000), and the study of the biogeography patterns of soil microbial communities may shed light on the response of microbial communities to climate change. Although environmental factors that would drive and influence the distributions of soil microbial communities remain under debate, such factors include climate, soil physicochemical characteristics and vegetation types (Bachar et al. 2010; Wu et al. 2009). All three of these components are arranged together and interact with each other. Climate factors include mean annual precipitation, mean annual temperature, mean annual evaporation, etc.

Mean annual precipitation and temperature always represent dominant factors that control the distributions of plants (Jobbágy and Jackson 2000). Mean annual precipitation is generally known to be a dominant driving factor of plants in the arid and semi-arid ecosystems; whether mean annual precipitation is a dominant factor for soil microbes or whether it linearly affects microbial community remains unknown. To test this hypothesis, we selected an arid region and a semiarid region, the northeastern margin of the Qinghai-Tibet Plateau, where mean annual precipitation is the dominant driving factor of vegetation (Wang et al. 2006; Zhu et al. 2010) which is then very likely to play a key role in influencing the microbial communities. The northeastern margin of the Qinghai-Tibet Plateau is an interesting area to test the feedback of the soil microbial community to mean annual precipitation, as there is a distinct gradient in mean annual precipitation from east to west varies from 36 to 394 mm yr⁻¹. Therefore, the objective of this study was to investigate the response of microbial communities to precipitation by studying the biogeographical patterns of soil microorganisms along a precipitation gradient in northeastern Tibet.

Materials and Methods

Sampling Sites

We investigated microbial communities and soils in a transect study across a 700-km-long precipitation gradient (MAP = $36-394 \text{ mm yr}^{-1}$) from the Qinghai lake to the Qaidam Basin in the northeast area of the Tibetan plateau (Figure 1). Fifteen sites were selected to represent three vegetation types that differ in physiognomy: alpine grasslands, alpine shrub and Qaidam desert. Across this precipitation gradient, the mean annual temperature (MAT) varies from 0°C to 3°C, with a tendency for slightly higher temperatures in the east. Before the fieldwork, we collected vegetation and relevant ecological information, and set up a sampling plan for the site locations.

During the sampling period, we selected representative types of the local soils to determine final sample sites with minimal human activities. The selected sites had a minimum amount of disturbance based on information provided by the site owners, although a light level of grazing occurred on



Fig. 1. Soil sampling site locations, mean annual precipitation (MAP) and mean annual temperature (MAT) of the microbial community studied. A) sampling site locations; B) MAP; C) MAT.

some sites. For those sites with a light level of grazing, grazed areas were excluded from sampling during our study period. Table 1 shows the location (latitude and longitude), elevation, MAP and MAT from 1989 to 2009, and the soil types for the 15 sites along a precipitation gradient in the northeastern Tibetan Plateau. Samples were taken during the winter season to minimize the potential influences of temperature on

soil microbial communities because microbes usually stop growth and are hibernate below 0° C.

Undisturbed soil samples were taken from a $1 \text{ m} \times 1 \text{ m}$ plot at each site in December 2009. Soil samples were extracted with a soil auger and carefully sliced for the following depth increments: 0–5, 5–10, 10–20, and 20–40 cm. Two set samples were extracted within each site. Soil samples were

Table 1. PLFAs used in this study as bioindicators

Marker	Marker for	Comments	Reference
i14:0 [*] , i15:0, a15:0, C15:1, 16:1w9c, 16: w7c, 16:1w5c, 16:1w3c, i17:0, a17:0, C17:1, cy17:0, C18:1, i19:0, cy19:0	Bacteria	Originally developed for sediments, more recently applied to forest litters	Federle et al. (1986) Frostegard et al. (1993) Tunlid et al. (1989)
18:1w9c, 18:2w6,9	Fungi	Good agreement with ergosterol	Federle et al. (1986)
I14:0, i15:0, a15:0, i16:0, i17:0, a17:0, 10Me16:0, 10Me17:0, 10Me18:0	Gram-positive bacteria	Branching at positions other than terminally considered a better marker	Zogg et al. (1997)
cy17:0, cy19:0, 16:1w9, 16:1w5, 18:1w7	Gram-negative bacteria	Generally regarded as good biomarkers	Mutabaruka et al. (2007)
10Me16:0, 10Me17:0, 10Me18:0	Actinomycete	Good agreement	Zelles (1997)
Total cyclopropyl/total w7 monounsaturated	Nutritional stress	Associated with transition to stationary growth	Zelles and Bai (1994) Reichardt et al. (1997)

*Nomenclature: Fatty acids are designated by the total number of carbon atoms and the number after the colon indicates the degree of unsaturation. The degree of unsaturation is followed by ωx , where x indicates the position of the double bond nearest to the aliphatic end. The prefixes a, i and cy refers to anteiso, iso and cyclopropyl branching fatty acid respectively; br indicates that the type of branching is unknown, while a number follow by Me indicates position of methyl group.

collected in sterile bags, packed in blue ice, and transported to the laboratory by air express within three days, where the soil samples were stored at -80° C before analysis. Subsamples for physical and chemical analysis were stored at 4°C.

Soil Physicochemical Analysis

The subsamples of soil were used for the determination of pH, total organic matter content (TOC), total nitrogen (TN) and soil texture. Typically, a fresh 30 g subsample was measured for gravimetric soil moisture after drying in a 70°C oven for 48 h. After adding an additional amount of deionized water (soil:water = 1:2.5) the soil pH was measured with a pH electrode (Sartorius PB-10). Soil texture (Clay/sand/ silt percentage) was determined with a Malvern Mastersizer 2000 analyzer, with a measurement range of 0.02 to 2000 Am. Total nitrogen was determined by Kjeldahl digestion and quantified with a continuous flow analyzer. Total organic carbon was measured with TOC analyzer (TOC-VCPH, Shimadzu, Japan). Water extractable ions were extracted from 5 g soil with 25 mL deionized water and measured by ion chromatography (ICS2500, Dionex Corporation). Soil analyses were carried out in duplicate. The analysis was repeated twice if the difference between the replicate values exceeded 10%. The outlying value was discarded if this difference was below 10%. The average of all four values was taken if the error remained above 10%.

Phospholipid Fatty Acid (PLFA) Extraction and Separation

Microbial PLFA lipids were extracted from lyophilized soil biomass using a single-phase Bligh and Dyer method (White et al. 1979), with minor modifications. Briefly, a freeze dried 5 g (n = 2) mixed soil sample was extracted twice with one

phase mixture of chloroform-methanol-phosphate buffer (1:2:0.8, v/v/v, pH 7.4) for a minimum 2 h by vigorous shaking. The extracted solutions were split into two phases by the addition of one volume of water and chloroform, respectively. The organic phase was recovered, and the extracted lipids were fractionated into neutral lipids, glycolipids and phospholipids on a silica acid (Unisil, Clarkson Chemical Co., Williamsport, PA, USA) column by consecutive elution with chloroform, acetone and methanol, respectively. The phospholipids were subjected to a mild alkaline methanolysis, which yielded the methylesters of ester-linked fatty acids (FAMEs), and then were frozen until analysis. All solvents and chemicals used were analytical grade. To remove lipid contaminants, all glassware used was heated overnight at 400°C.

Bacterial biomass was estimated from the summed concentrations of the following PLFAs: i14:0, i15:0, a15:0, C15:1, i16:0, 16:1 ω 9c, 16: ω 7c, 16:1 ω 5c, 16:1 ω 3c, i17:0, a17:0, C17:1, cy17:0, C18:1, i19:0, cy19:0 (Federle et al. 1986; Frostegard et al. 1993; Tunlid et al. 1989). Fungal biomass was estimated from concentrations of the following PLFAs: 18:1w9c, 18:2w6,9 (Federle et al. 1986) (Table 1).

GC-MS Analysis

All PLFA samples were analyzed by capillary gas chromatography, using a Hewlett-Packard 7890A GC with a flame ionization detector. The column was an HP-5 capillary column (30 m; 0.25-mm ID; 0.25- μ m film thickness), and hydrogen was used as the carrier gas, with a flow rate of 3.5 mL min⁻¹. The splitless mode was selected in injection. The injector and detector were maintained at 320°C, and the column temperature was programmed from 80°C for 1 min to 280°C for 10 min at a ramping rate of 3°C min⁻¹, with each run lasting approximately 77 min. Tentative peak identifications before mass spectrometric (MS) analysis were based on comparison of retention times with standard compounds (Bacterial Acid Methyl Esters Mix; Supelco, Bellefonte, PA, USA). FAMEs quantification was performed by adding methyl nonadecanoate as an internal standard before GC injections.

Selected PLFA samples were analyzed using a Hewlett-Packard 6890 gas chromatograph (GC) coupled to a Hewlett-Packard 5973 mass selective detector (MSD) to confirm compound identification. The GC conditions were those described above, but helium was used as the carrier gas at a linear velocity of 28 cm/sec, with the injector operating at a constant flow of 0.9 mL min⁻¹. The oven temperature was programmed from 80 to 280° C at 3° C min⁻¹, with initial and final hold times of 1 and 30 min, respectively. The MSD was operated with an ionization energy of 70 eV, a source temperature of 230°C, and an electron multiplier voltage of 1800 V over the mass range 35-550 Daltons. Data were collected in the full-scan and multiple ion detection (MID) mode. MS identifications of fatty acid methyl esters were based on comparison with spectra from standard compounds (Bacterial Acid Methyl Esters Mix; Supelco, Bellefonte, PA, USA) or with spectra reported in the literature.

Statistical Analysis

Differences in PLFA profiles and physicochemical characteristics of soil among the fifteen sites were analyzed using redundancy analysis (RDA) in the CANOCO 4.5 program, which is a constrained ordination method, with the ordination axes constrained to be linear combinations of environmental factors. Mole percentages (mol%) of individual fatty acids were used in all the analyses except for total PLFAs, which was expressed as nmol g^{-1} soil, on a dry weight basis. All data were standardized before analysis. Available environmental factors were filtered by VIF (variance inflation factor). The correlation and regression analysis between precipitation and the microbial community were analyzed using SPSS 17.0 for Windows (SPSS Inc.). For all analyses, statistical significance was determined at the P < 0.05 level. Sigma plot 9.0 (Systat Software Inc.) and Coreldraw X4 (Corel corporation) were used to draw the diagrams.

Results

Soil Physicochemical Properties

All the sampling sites extended along a 700-km range in latitude from Qinghai Lake in the east to the Yiliping area in the west, with the mean annual precipitation significantly decreasing from east to west (36 to 394 mm yr⁻¹ (Figure 1)). Twelve soil physicochemical factors were measured in soil samples, and they were used for the analysis of microbial community composition (Table 2). Most soil characteristics varied with location, resulting in significant differences among sampling sites. Along the precipitation gradient from the dry to wet sites, the TOC content in the surface layer (0–5 cm) significantly increased from 0.30% in stands with 36 mm yr⁻¹ of precipitation in desert area to 5.39% in stands with more than 394 mm yr⁻¹ of precipitation in the alpine meadow ecosystem.

A similar increasing trend was found in the soil profiles from the 5-10, 10-20 and 20-40 cm depths, where the TOC increased from 0.28% in the dry stands to 3.48% in the more moist stands at 5-10 cm soil depth. Soil C/N ratios remained relatively constant along the precipitation gradient, except for site 9, which was located in a wetland and thus was affected by moving groundwater. In contrast, soil pH values and soil sand content in the 0-5 cm depth soils gradually decreased, coupled with a significant decrease of soil Cl⁻, SO_4^{2-} and NO_3^{-} content along the precipitation gradient from the dry to the wet sites. The range of soil pH was between 7.13 and 9.41, due to the presence of carbonates. The texture of the soils was generally dominated by silt and sand, with a mean value exceeding 95% (Table 2). When the amount of precipitation was less than 50 mm, the mean clay content was lowest (1%), and the anion contents were also higher than other sites.

TOC content, TN and soil C/N ratios all decreased with increasing soil depth at all sites, with relatively large amounts of organic matter C and N in the top 0–5-cm layer and lower TOC content and TN in the three lower layers (P < 0.05). In contrast, the soil water content general increased with increasing soil depth. TOC and TN decreased as the soil depth increased, and the C/N ratio was usually between 4 to 10. Meanwhile, the soil anion content (Cl⁻, SO₄^{2–} and NO₃⁻) slowly decreased in the soil profiles from 0–5 cm down to the 20–40 cm depth at each site. In general, soil physicochemical properties did not differ significantly among different soil depths, but the tendency was clear despite large differences among the soils (Table 2).

All in all, precipitation significantly correlated with soil physicochemical properties (Figure 2). TN and TOC were significantly related to MAP (R = 0.699, P < 0.001; R = 0.658, P < 0.001, respectively). Additionally, moisture and silt were positively correlated with MAP (R = 0.405, P < 0.05; R = 0.495, P < 0.05, respectively). A similar negative relationship was found between MAP, pH, sand, Cl⁻, and SO₄²⁻ (R = 0.448, P < 0.05; R = 0.482, P < 0.05; R = 0.545, P < 0.05; R = 0.627, P < 0.05, respectively).

Microbial Biomass and Community Composition

Microbial biomass, expressed as total PLFAs, significantly decreased with decreasing mean annual precipitation (Figure 3). Along the precipitation gradient from the dry to the wet sites, total microbial biomass per gram of soil was highest in stands with 394 mm yr⁻¹ and lowest in stands with stands less than 36 mm yr⁻¹. Generally speaking, the highest biomass was found in alpine grassland areas, the lowest biomass was found in the Qaidam basin desert areas, which are strongly impacted by groundwater (Figure 3). Soil bacteria biomass was only strongly correlated with MAP at the soil surface (0–10 cm), but not in deeper soils (10–40 cm). In the semi-arid areas (MAP 180–394 mm yr⁻¹), the soil bacteria

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Table 2. Main physicochemical soil properties at different sampling sites

SO ₄ ²⁻ (mg/kg)	0.03 (0.00) 0.03 (0.00) 0.03 (0.00) 0.03 (0.00)	$\begin{array}{c} 0.05 \\ 0.05 \\ 0.10 \\ 0.54 \\ 0.10 \\ 0.78 \\ 0.13 \\ 0.$	0.02 (0.00) 0.02 (0.00) 0.02 (0.00) 0.03 (0.00)	0.03 (0.00) 0.03 (0.00) 0.02 (0.01) 0.05 (0.01)	$\begin{array}{c} 0.03 \\ 0.01 \\ 0.00 \\ 0.$	$\begin{array}{c} 0.70 \\ 0.70 \\ 0.27 \\ 0.04 \\ 0.35 \\ 0.06 \\ 0.21 \\ 0.03 \\ 0.03 \\ \end{array}$	$\begin{array}{c} 0.08 \\ 0.08 \\ 0.04 \\ 0.01 \\ 0.03 \\ 0.01 \\ 0.00 \\ 0.$	$\begin{array}{c} 0.06 \ (0.01) \\ 0.03 \ (0.00) \\ 0.02 \ (0.00) \\ 0.02 \ (0.00) \end{array}$	$\begin{array}{c} 1.09 & (0.23) \\ 0.88 & (0.14) \\ 0.90 & (0.15) \\ 1.11 & (0.21) \end{array}$	$\begin{array}{c} 0.03 & (0.01) \\ 0.38 & (0.12) \\ 1.38 & (0.26) \\ 1.08 & (0.32) \end{array}$
NO ₃ ⁻ (mg/kg)	0.01 (0.00) 0.03 (0.01) 0.03 (0.01)	0.01 (0.00) 0.01 (0.00) 0.02 (0.00) 0.01 (0.00)	0.01 (0.00) 0.02 (0.00) 0.02 (0.00)	0.01 (0.00) 0.01 (0.00) 0.01 (0.00)	$0.04 (0.00) \\ 0.03 (0.00) \\ 0.05 (0.01) \\ 0.01 (0.00) \\ 0.01 $	0.00 (0.00) 0.00 (0.00) 0.01 (0.00)	0.01 (0.00) 0.01 (0.00) 0.01 (0.00) 0.02 (0.00)	$\begin{array}{c} 0.01 \\ 0.01 \\ 0.01 \\ 0.02 \\ 0.00 \\ 0.02 \\ 0.00 \\ 0.00 \\ \end{array}$	$\begin{array}{c} 1.12 \\ 0.42 \\ 0.38 \\ 0.38 \\ 0.14 \\ 0.27 \\ 0.23 \\ \end{array}$	$\begin{array}{c} 0.00 \\ 0.00 \\ 0.00 \\ 0.01 \\ 0.01 \\ 0.00 \\ 0.01 \\ 0.00 \\ \end{array}$
Cl ⁻ (mg/kg)	$\begin{array}{c} 0.04 & (0.01) \\ 0.04 & (0.01) \\ 0.04 & (0.02) \\ 0.05 & (0.01) \end{array}$	$\begin{array}{c} 0.10 \\ 0.10 \\ 0.20 \\ 0.30 \\ 0.01 \\ 0.48 \\ 0.05 \\ 0.$	$\begin{array}{c} 0.03 \\ 0.03 \\ 0.01 \\ 0.02 \\ 0.01 \\ 0.03 \\ 0.01 \\ 0.$	$\begin{array}{c} 0.05 \\ 0.04 \\ 0.01 \\ 0.03 \\ 0.01 \\ 0.$	0.06(0.02) 0.06(0.02) 0.05(0.01) 0.01(0.00)	$\begin{array}{c} 0.83 \\ 0.25 \\ 0.25 \\ 0.04 \\ 0.39 \\ 0.04 \\ 0.03 \\ 0.01 \\ 0.03 \\ 0.$	$\begin{array}{c} 0.16 \\ 0.03 \\ 0.03 \\ 0.01 \\ 0.03 \\ 0.01 \\ 0.$	$\begin{array}{c} 0.04 & (0.01) \\ 0.03 & (0.01) \\ 0.03 & (0.01) \\ 0.03 & (0.01) \\ 0.03 & (0.01) \end{array}$	2.53 (0.84) 1.42 (0.21) 1.47 (0.21) 1.63 (0.31)	$\begin{array}{c} 0.95 \\ 0.47 \\ 0.47 \\ 0.48 \\ 0.14) \\ 0.35 \\ 0.12) \\ 0.35 \\ 0.12) \end{array}$
Sand (%)	34.13 (5.68) 33.12 (3.85) 23.50 (1.62) 30 67 (5 76)	64.83 (4.67) 69.88 (5.90) 64.53 (4.51) 24.25 (2.75)	45.89 (3.24) 50.12 (6.58) 43.38 (6.88) 55.12 (8.64)	27.69 (4.48) 26.55 (6.54) 23.52 (2.61) 17 27 (8.66)	12.58 (5.44) 20.86 (5.04) 13.50 (4.45) 18.03 (4.68)	26.31 (6.90) 24.72 (6.25) 30.67 (3.06) 27.39 (1.01)	$\begin{array}{c} 40.14 \\ 40.53 \\ 47.95 \\ 3.88 \\ 28.32 \\ 4.97 \\ \end{array}$	$\begin{array}{c} 12.58 (3.04) \\ 20.86 (1.87) \\ 13.50 (1.52) \\ 18.03 (1.13) \end{array}$	$\begin{array}{c} 19.68 \\ (1.72) \\ 26.53 \\ (0.59) \\ 25.44 \\ (3.34) \\ 13.02 \\ (5.33) \end{array}$	47.2 (2.26) 52.73 (5.59) 39.17 (2.67) 37.49 (1.42)
Silt (%)	54.19 (6.85) 53.38 (5.02) 73.08 (0.69) 56 77 (6 97)	3.09 (11.86) 8.58 (12.59) 3.26 (11.99) 70.85 (1.58)	58.15 (5.18) 58.86 (6.61) 56.23 (7.81) 51 59 (4.58)	58.15 (5.18) 58.86 (6.61) 72.10 (3.83) 9.28 (10.05)	83.93 (9.51) 77.05 (6.37) 4.41 (10.61) 78.57 (8.95)	73.65 (7.76) 74.84 (7.45) 58.51 (2.99) 71.01 (0.93)	57.58 (4.32) 57.58 (4.32) 57.85 (2.66) 51.06 (2.87) 58.42 (5.88)	3.93 (12.04) 77.05 (2.60) 84.41 (3.22) 78.57 (0.48)	78.08 (1.06) 71.26 (0.83) 74.56 (2.03) 84.71 (0.88)	51.95 (1.90) 46.37 (1.56) 58.70 (2.08) 59.19 (1.93)
Clay (%)	1.68 (0.16) (0.19) (0.19) (0.19) (0.19) (0.19) (0.19) (0.19) (0.19) (0.19) (0.19) (0.19) (0.11) (0.1	$\begin{array}{c} 2.08 \\ 0.43 \\ 1.54 \\ 0.31 \\ 2.21 \\ 0.52 \\ 3.221 \\ 0.52 \\ 3.221 \\ 0.52 \\ 3.221 \\ 0.52 \\ 3.221 \\ 0.52 \\ 3.221 \\ 0.52 \\ 3.221 \\ 0.52 \\ 3.221 \\ 0.521 \\ 0.521 \\ 0.5$	2.08 (0.23) 1.54 (0.69) 4.59 (0.06) 4.38 (0.22)	4.16 (0.71) 4.59 (0.06) 4.38 (0.22) 3.45 (0.39) 7	3.49 (0.06) 2.09 (1.33) 2.09 (0.16) 3.40 (0.27)	0.04 (0.01) 0.44 (0.02) 0.82 (0.07) 0.83 0.08)	2.28 (0.56) 1.62 (0.03) 0.99 (0.03) 3.26 (0.65)	3.49 (1.00) 8 2.09 (0.73) 7 2.09 (0.69) 8 3.40 (0.35) 7	2.24 (0.04) 2.21 (0.24) 1.31 (0.35) 2.27 (0.39)	0.85 (0.03) 0.90 (0.03) 2.13 (0.09) 3.32 (0.15)
Hq	8.07 (0.10) 8.25 (0.35) 8.45 (0.17) 8.44 (0.15)	8.93 (0.15) 8.35 (0.08) 8.44 (0.05)	8.17 (0.17) 8.25 (0.16) 8.36 (0.01) 8.43 (0.02)	7.94 (0.16) 8.04 (0.07) 8.16 (0.01) 8 39 (0 14)	7.63 (0.12) 7.72 (0.02) 8.06 (0.01) 8.16 (0.08)	8.89 (0.17) 8.93 (0.11) 9.11 (0.01) 9.01 (0.09)	7.97 (0.14) 7.98 (0.34) 8.60 (0.09) 7.13 (0.07)	7.79 (0.07) 7.95 (0.20) 8.06 (0.03) 8.29 (0.20)	8.05 (0.13) 8.16 (0.03) 8.11 (0.01) 7.95 (0.21)	8.14 (0.31) 8.69 (0.24) 7.98 (0.18) 8.77 (0.24)
Moisture (%)	20.38 (2.12) 44.37 (12.00) 24.85 (5.17) 21 15 (1.62)	26.35 (6.49) 22.58 (4.77) 26.35 (6.49)	2.71 (1.87) 7.15 (2.70) 7.99 (2.14) 14 50 (1.83)	6.36 (4.71) 6.36 (4.71) 16.69 (1.95) 13.85 (0.23) 14.77 (1.16)	19.97 (8.62) 22.98 (4.29) 24.97 (4.26) 23.17 (4.55)	31.19 (8.62) 30.51 (4.29) 27.20 (4.26) 42.12 (4.55)	50.81 (3.19) 50.81 (3.19) 64.83 (1.91) 49.35 (2.52)	45.22 (1.29) 39.04 (2.73) 40.12 (4.26) 36.44 (2.42)	$\begin{array}{c} 13.20 \\ 13.26 \\ 0.43 \\ 11.09 \\ 11.09 \\ 1.71 \\ 14.73 \\ 0.39 \end{array}$	8.16 (3.09) 9.79 (3.87) 8.98 (2.33) 9.25 (1.81)
C/N	8.72 (1.05) 7.73 (0.02) 7.84 (0.25) 7.78 (0.20)	5.49 (0.22) 5.75 (1.70) 6.27 (0.03) 6.48 (0.23)	$\begin{array}{c} 10.68 \\ 24.00 \\ 10.12 \\ 10.12 \\ 1.78 \\ 9.54 \\ 3.12 \\ \end{array}$	6.29 (0.15) 6.68 (0.33) 6.50 (0.04) 6.13 (0.04)	$\begin{array}{c} 7.21 \\ 7.21 \\ 0.07 \\ 7.31 \\ 6.97 \\ 0.47 \\ 6.84 \\ 0.41 \\ \end{array}$	7.06 (0.85) 8.04 (0.69) 8.13 (0.56) 8.31 (1.63)	6.27 (1.18) 5.97 (1.23) 3.68 (1.80) 3.11 (1.25)	$\begin{array}{c} 9.72 \\ 0.93 \\ 9.40 \\ 0.45 \\ 9.24 \\ 0.74 \\ 9.22 \\ 0.89 \end{array}$	7.48 (1.09) 5.26 (0.32) 5.07 (1.45) 5.56 (0.09)	4.43 (1.78) 5.68 (1.13) 8.14 (0.14) 6.40 (0.63)
(%) (%)	$\begin{array}{c} 0.62 & (0.03) \\ 0.45 & (0.04) \\ 0.28 & (0.07) \\ 0.20 & (0.07) \end{array}$	0.35(0.10) 0.34(0.04) 0.34(0.01) 0.21(0.03)	$\begin{array}{c} 0.24 \\ 0.24 \\ 0.09 \\ 0.03 \\ 0.22 \\ 0.03 \\ 0.25 \\ 0.47 \end{array}$	$\begin{array}{c} 0.81 \\ 0.65 \\ 0.65 \\ 0.03 \\ 0.45 \\ 0.02 \\ 0.41 \\ 0.03 \\ 0.$	0.56(0.06) 0.69(0.04) 0.68(0.08) 0.58(0.03)	$\begin{array}{c} 0.19 \\ 0.19 \\ 0.16 \\ 0.05 \\ 0.16 \\ 0.05 \\ 0.20 \\ 0.01 \end{array}$	$\begin{array}{c} 0.51 \\ 0.51 \\ 0.69 \\ 0.69 \\ 0.62 \\ 0.05 \\ 0.61 \\ 0.06 \\ \end{array}$	$\begin{array}{c} 0.81 & (0.16) \\ 0.77 & (0.14) \\ 0.77 & (0.01) \\ 0.46 & (0.04) \end{array}$	$\begin{array}{c} 0.17 & (0.02) \\ 0.16 & (0.01) \\ 0.09 & (0.02) \\ 0.11 & (0.01) \end{array}$	$\begin{array}{c} 0.06 & (0.03) \\ 0.04 & (0.01) \\ 0.04 & (0.01) \\ 0.04 & (0.00) \\ \end{array}$
TOC (%)	$\begin{array}{c} 5.39(0.47)\\ 3.48(0.27)\\ 2.19(0.65)\\ 1.58(0.61)\end{array}$	$\begin{array}{c} 1.93 \ (0.50) \\ 1.94 \ (0.50) \\ 2.13 \ (0.25) \\ 1.38 \ (0.25) \end{array}$	$\begin{array}{c} 2.55(0.09)\\ 2.16(0.03)\\ 2.19(0.04)\\ 2.41(0.31)\\ \end{array}$	5.06 (0.57) 5.06 (0.57) 4.31 (0.41) 2.93 (0.10) 2.50 (0.16)	4.04 (0.41) 5.05 (0.24) 4.71 (0.33) 3.96 (0.05)	$\frac{1.37(0.07)}{1.30(0.87)}$ $\frac{1.28(0.70)}{1.28(0.70)}$	$\frac{3.18}{2.29} \underbrace{(0.98)}_{(0.61)}$	7.83 (0.46) 7.27 (0.87) 7.14 (0.65) 4.22 (0.08) 7.14 (0.68) 7.1	$\begin{array}{c} 1.27 (0.27) \\ 0.82 (0.02) \\ 0.46 (0.29) \\ 0.58 (0.04) \end{array}$	$\begin{array}{c} 0.28 (0.10) \\ 0.23 (0.08) \\ 0.35 (0.06) \\ 0.28 (0.04) \end{array}$
Soil depth (cm)	$\begin{array}{c} 0-5\\ 5-10\\ 10-20\\ 20-40\end{array}$	20-5 5-10 10-20 20-40	0-5 5-10 10-20 20-40	0-5 5-10 10-20	0-5 5-10 10-20 20-40	$\begin{array}{c} -0 \\ 5-10 \\ 10-20 \\ 20-40 \end{array}$	$\begin{array}{c} 0-5\\ 5-10\\ 10-20\\ 20-40\end{array}$	$\begin{array}{c} 0-5\\ 5-10\\ 10-20\\ 20-40\end{array}$	$\begin{array}{c} 0-5\\ 5-10\\ 10-20\\ 20-40\end{array}$	$\begin{array}{c} 0-5\\ 5-10\\ 10-20\\ 20-40\end{array}$
Vegetation type	Alpine grasslands	Alpine grasslands	Alpine grasslands	Alpine grasslands	Alpine grasslands	Alpine grasslands	Alpine grasslands	Alpine grasslands	Alpine shrub	A lpine shrub
Elevation (m)	3149	3311	3272	3239	3230	3199	3817	3804	2955	3354
MAT (°C) ^B	1.29	-0.06	0.31	-	2.09	1.5	-0.97	-2.31	4.65	2.33
MAP (mm) ^A	394.5	383.5	361.8	352.3	327.3	322	312.6	300.4	210.4	206.5
Sample site	-	23	0	б	22	4	21	Ś	9	20

(Continued on next page)

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 Table 2. Main physicochemical soil properties at different sampling sites (Continued)

	କ୍ଳ୍ୟର	6446		<u>ି</u> କ କ କ କ କ	ତ୍ତ୍ତ୍ତ୍ତ୍
SO4 ^{2–} (mg/kg	0.05 (0.0 0.09 (0.0 0.10 (0.0 0.12 (0.0	0.80 (0.1 1.03 (0.1 1.50 (0.2 2.71 (0.7	5.66 (1.2 4.43 (1.2 0.07 (0.0 2.05 (0.3	$\begin{array}{c} 0.17 \\ 0.18 \\ 0.18 \\ 0.16 \\ 0.0 \\ 0.12 \\ 0.0 \end{array}$	0.35 (0.0 0.01 (0.0 0.03 (0.0 0.02 (0.0
NO3 ⁻ (mg/kg)	$\begin{array}{c} 0.02 \ (0.00) \\ 0.07 \ (0.01) \\ 0.08 \ (0.01) \\ 0.06 \ (0.02) \end{array}$	0.00 (0.00) 0.00 (0.00) 0.00 (0.00) 0.00 (0.00)	$\begin{array}{c} 0.43 \ (0.14) \\ 0.03 \ (0.01) \\ 0.00 \ (0.00) \\ 0.01 \ (0.00) \end{array}$	0.00 (0.00) 0.00 (0.00) 0.00 (0.00) 0.00 (0.00)	0.00 (0.00) 0.04 (0.02) 0.00 (0.00) 0.00 (0.00)
Cl ⁻ (mg/kg)	$\begin{array}{c} 0.10 \ (0.03) \\ 0.16 \ (0.04) \\ 0.21 \ (0.06) \\ 0.24 \ (0.06) \end{array}$	$\begin{array}{c} 3.57 \\ 2.02 \\ 1.90 \\ 1.75 \\ 0.14 \\ 0.14 \end{array}$	$\begin{array}{c} 1.30 & (0.26) \\ 1.25 & (0.26) \\ 1.25 & (0.25) \\ 1.12 & (0.19) \end{array}$	$\begin{array}{c} 0.16 \ (0.03) \\ 0.07 \ (0.02) \\ 0.08 \ (0.02) \\ 0.05 \ (0.02) \end{array}$	$\begin{array}{c} 1.30 \ (0.23) \\ 0.62 \ (0.23) \\ 0.10 \ (0.03) \\ 0.03 \ (0.01) \end{array}$
Sand (%)	98.58 (5.07) 98.09 (2.25) 95.72 (2.65) 98.27 (2.20)	64.59 (3.68) 59.81 (7.48) 54.92 (6.16) 66.70 (2.04)	83.34 (5.68) 83.64 (4.13) 83.15 (10.69) 82.82 (15.62)	45.64 (5.66) 64.42 (4.86) 62.87 (8.73) 48.97 (3.54)	91.87 (6.68) 90.48 (10.21) 92.85 (7.13) 94.42 (9.96)
Silt (%)	1.42 (0.57) 1.91 (0.55) 4.28 (1.65) 1.73 (0.81)	34.63 (7.77) 39.38 (7.49) 43.70 (6.17) 32.85 (2.27)	$10.80(2.28) \\ 11.21(3.21) \\ 12.02(3.36) \\ 11.95(2.54)$	53.43 (6.89) 35.19 (4.57) 36.24 (5.43) 49.32 (9.92)	5.93 (1.26) 7.05 (2.83) 5.53 (1.48) 4.28 (2.11)
Clay (%)	$\begin{array}{c} 0.00 \ (0.00) \\ 0.00 \ (0.00) \\ 0.00 \ (0.00) \\ 0.00 \ (0.00) \end{array}$	$\begin{array}{c} 0.78 \\ 0.13 \\ 0.81 \\ 1.38 \\ 0.11 \\ 0.45 \\ 0.09 \end{array}$	5.86 (0.64) 5.15 (0.82) 4.83 (0.24) 5.23 (0.88)	$\begin{array}{c} 0.93 \\ 0.03 \\ 0.39 \\ 0.39 \\ 0.89 \\ 0.09 \\ 1.71 \\ 0.43 \end{array}$	2.20 (0.88) 2.47 (0.56) 1.62 (0.47) 1.30 (0.32)
Hq	9.24 (0.26) 9.40 (0.41) 9.41 (0.28) 9.38 (0.48)	8.96 (0.47) 8.84 (0.28) 8.46 (0.13) 8.24 (0.05)	8.26 (0.10) 8.10 (0.04) 8.46 (0.28) 8.54 (0.07)	8.03 (0.98) 7.85 (1.25) 7.84 (1.65) 8.03 (2.24)	9.09 (2.51) 9.29 (2.88) 9.01 (1.62) 8.85 (1.45)
Moisture (%)	$\begin{array}{c} 0.53 \ (0.19) \\ 1.67 \ (0.58) \\ 3.51 \ (1.20) \\ 3.06 \ (0.93) \end{array}$	$\begin{array}{c} 1.80\ (0.81)\\ 3.75\ (1.60)\\ 2.98\ (0.45)\\ 4.59\ (1.15)\end{array}$	$\begin{array}{c} 0.39 \ (0.02) \\ 7.21 \ (0.66) \\ 5.57 \ (0.83) \\ 4.87 \ (0.57) \end{array}$	58.74 (3.25) 59.02 (6.86) 47.78 (5.66) 50.76 (10.23)	11.39 (2.31) 30.71 (4.73) 31.85 (5.32) 28.57 (6.41)
C/N	16.06 (1.94) 27.07 (2.00) 30.30 (2.13) 38.40 (12.3)	5.33 (0.44) 6.90 (0.02) 5.59 (0.35) 6.47 (0.15)	3.97(0.10) 6.85(2.11) 8.58(0.32) 9.94(1.99)	8.99 (0.25) 5.81 (0.56) 10.09 (0.88) 8.57 (0.65)	7.74 (0.23) 7.15 (0.31) 9.07 (0.42) 8.33 (0.68)
TN (%)	$\begin{array}{c} 0.02 \ (0.00) \\ 0.01 \ (0.00) \\ 0.00 \ (0.00) \\ 0.01 \ (0.00) \end{array}$	$\begin{array}{c} 0.04 \ (0.00) \\ 0.05 \ (0.01) \\ 0.04 \ (0.00) \\ 0.03 \ (0.00) \end{array}$	$\begin{array}{c} 0.10 \ (0.00) \\ 0.03 \ (0.00) \\ 0.03 \ (0.00) \\ 0.03 \ (0.00) \end{array}$	$\begin{array}{c} 0.66 \ (0.02) \\ 0.75 \ (0.04) \\ 0.36 \ (0.05) \\ 0.40 \ (0.07) \end{array}$	$\begin{array}{c} 0.04 & (0.00) \\ 0.03 & (0.00) \\ 0.03 & (0.00) \\ 0.03 & (0.00) \end{array}$
TOC (%)	$\begin{array}{c} 0.27(0.10)\\ 0.38(0.02)\\ 0.30(0.14)\\ 0.19(0.03)\end{array}$	$\begin{array}{c} 0.22 \ (0.03) \\ 0.36 \ (0.07) \\ 0.21 \ (0.01) \\ 0.21 \ (0.03) \end{array}$	$\begin{array}{c} 0.38 \\ 0.23 \\ 0.23 \\ 0.27 \\ 0.03 \\ 0.34 \\ 0.07 \end{array}$	$\begin{array}{c} 5.93\ (0.68)\\ 4.33\ (0.55)\\ 3.65\ (0.54)\\ 3.45\ (0.46)\end{array}$	$\begin{array}{c} 0.30 \ (0.02) \\ 0.28 \ (0.04) \\ 0.25 \ (0.04) \\ 0.25 \ (0.01) \end{array}$
Soil depth (cm)	$\begin{array}{c} 0-5\\ 5-10\\ 10-20\\ 20-40\end{array}$	$\begin{array}{c} 0-5\\ 5-10\\ 10-20\\ 20-40 \end{array}$			
Vegetation type	Alpine shrub	Alpine shrub	Qaidam basin desert	Qaidam basin desert	Qaidam basin desert
Elevation (m)	2861	3002	2915	2819	2845
MAT (°C) ^B	5.97	1.19	4.59	2.5	4.74
MAP (mm) ^A	181.1	114.8	59.7	37.3	36.8
Sample site	7	×	18	6	19

A: Mean annual precipitation was calculated since 1989–2009; B: Mean annual temperature was calculated since 1989–2009.

biomass decreased with increasing soil depth, whereas the soil bacteria biomass was mainly concentrated in the deeper soils of the arid areas (MAP $< 180 \text{ mm yr}^{-1}$).

Overall, the biomass of Gram-negative bacteria (G⁻), Gram-positive bacteria (G⁺), and actinomycete bacteria all decreased concomitantly with decreasing precipitation (P = 0.01, 0.03 and 0.03, respectively), whereas the decreasing trend of fungal biomass was relatively gentle (P < 0.01). The G⁻, G⁺, actinomycete and fungal biomass of soils was also positively correlated with MAP at the soil surface (0–10 cm), but there was no correlation with MAP in soils at 10–40 cm depth. Microbial communities in the semiarid-arid and arid soils were dominated by G⁻; the highest relative abundance of G⁻ was observed among the semiarid and arid ecosystems compared to the other three types of microbes, which ranged up to 82% among the 15 sites, and was accompanied by a lower relative abundance of actinomycete bacteria and the lowest abundance of fungi biomarkers.

lowest abundance of fungi biomarkers. A linear correlation ($R^2 = 0.528$; n = 15; P < 0.001) was found between total bacterial PLFA in the 0–5-cm top layer and the precipitation gradients, but the linearly correlated relationship between total bacterial PLFA and the precipitation gradients weakened as soil depth increased. The biomass of G^+ , G^- , actinomycetes or fungi also correlated linearly with the precipitation gradients in the 0–5, 5–10 and 10– 20 cm soil layers, respectively. However, the ratios of fungi/ bacteria (F/B), G^+/G^- , and total cyclopropyl/total ω 7 monounsaturated (cy/pre) showed no linear correlation with precipitation gradients in the different soil layers. Overall, the ratio of F/B and G⁺/G⁻ increased with decreasing precipitation but increased with increasing soil depth.

In the 0–5-cm soil depth, the ratio of F/B was strongly correlated with C/N ratio (R = 0.625, P = 0.013) and pH (R = 0.522, P = 0.04), and cy/pre ratio was highly related to precipitation for this soil depth (R = -0.543, P = 0.036).

In the 5–10 cm soil depth, the F/B ratio was strongly positively correlated with the chloride ($\mathbf{R} = 0.691, P = 0.004$), nitrate (R = 0.952, P < 0.001) and sulfate (R = 0.827, P < 0.001) (0.001) ion concentrations, and the ratio of cy/pre was highly related to precipitation (R = -0.674, P = 0.006). In the 10-20-cm soil depth, the F/B ratio was negatively correlated with precipitation (R = -0.544, P = 0.036) and the cy/pre ratio was highly related to precipitation (R = -0.591, P =0.019). In the 20–40 cm soil depth, the ratio of F/B was also strongly related to precipitation (R = -0.55, P = 0.034) and strongly positively correlated with sulfate ion (R = 0.527, P = 0.04) concentration; the cy/pre ratio had no correlation with environmental factors in this soil depth. There was no obvious correlation between the G^+/G^- ratio and environmental factors in the four soil depths. The strong correlation between the cy/pre ratio and precipitation indicates that cy/ pre ratio could be a good indicator for precipitation stress.

Discussion

Along the precipitation gradient, many soil physicochemical properties changed simultaneously. With decreasing precipitation, the soil water content decreased significantly (Figure 2). Soil water content is an important factor that governs the bioavailability of nutrients (Stanley 1995), nutrient transportation (Hansel et al. 2008), oxygen diffusion (Skopp et al. 1990) and other aspects of soil biogeochemistry. With decreasing precipitation, the annual net primary productivity of vegetation decreases (Lin et al. 2013), which may then produce less litter or nutrients for soil microbes. Different types of vegetation produce litter of different quality and quantity.

The northeastern Tibetan plateau has three main vegetation regions: alpine grasslands, alpine shrub and the Qaidam desert. The differences of litter quality among the three types of vegetation may affect the microbial community structure but may not have as great an effect on the soil microbial biomass. Soil microbes are dominantly heterotrophic microbes that depend on substrate nutrients. Thus, precipitation may indirectly affect microbes by shaping the net primary productivity of vegetation.

In the studied areas, there is an obvious spatial precipitation gradient from 36 to 394 mm yr^{-1} , while the MAT was no more than 6°C. To minimize the temperature effect, we sampled soils in winter when microbes survive at a freezing temperature. At a depth of 0-5 cm, the bacteria and fungi biomass showed a strongly positive response to precipitation (R = 0.708 and 0.496, respectively), which is consistent with studies by Steinberger et al. (1999). They found that microbial biomass was highly positively related to precipitation in the surface soil of the Judean Desert. In contrast, Wu et al. (2009) found that MAP was not a major factor influencing the size of the soil microbial biomass where the MAP varied from 550 mm yr^{-1} to 1690 mm yr⁻¹; in abundant precipitation areas, precipitation is not the dominant limiting factor that affects soil microbial communities. In contrast, precipitation would become a dominant driving force for microbial communities when precipitation descends to a threshold that limits ecosystems, especially for semi-arid and arid ecosystems.

Previous studies also showed that soil moisture can influence the composition of the soil bacterial and fungal communities (Schimel et al. 1999; Wilkinson et al. 2002), but soil moisture variability is only likely to be one of the most important factors that would affect microbial community composition at the soil surface (Brockett et al. 2012). In arid and semi-arid areas, soil moisture was strongly correlated with precipitation. With increasing soil depth, the correlation between microbial biomass and precipitation weakened, which is in line with previous research. It is very likely that groundwater has a greater impact in the deeper soils, or that the amount of precipitation is simply too low to permeate into deeper soil.

Precipitation may affect microbial biomass by constraining nutrient availability. Excessive precipitation may also reduce the biomass due to an increasing constraint on root respiration. As a result, few nutrients would have been washed away, and some bacterial cells are also more likely to rupture after precipitation due to osmotic shock (Landesman and Dighton 2011). In arid areas, however, soil moisture is strongly correlated with precipitation. With more rainfall available, vegetation will have a better growth rate, and the available nutrients will further spur growth and biomass production of bacteria. The main factors affecting the soil microbial community were the C/N ratio, soil moisture, soil pH and precipitation (Bååth and Anderson 2003; Fierer and Jackson 2006). The soil C/N ratio was an important indicator of nutritional status, which depends on the litter of vegetation at the surface. The microbial biomass was decreased 2.5 times, on average, from the 0–5 cm depth to the 5–10 cm depth. The lower content of microbial biomass in deeper soil layers was attributed to a lower input of organic matter, in particular a lower input of available C (Allison et al. 2007; Steenwerth et al. 2002). G⁻ bacteria are favored by the inputs of fresh organic material and are thus more abundant in the surface soil, where the soil organic carbon concentration and quality are higher compared to deeper soils (Fierer and Schimel 2002; Griffiths et al. 1999).

Actinomycetes are filamentous G^+ bacteria that utilize recalcitrant compounds, too. The bacterial biomass was greater than the fungal biomass at all the sites, which might be explained by soil physical properties. Bacteria could grow better in low C/N soil (<30), whereas fungi use substrates with a wider range of C/N ratios (>38) than bacteria (Sterner and Elser 2002), which was consistent with the soil properties where the PLFA composition was changed along the soil pH gradient (Rousk et al. 2010). This study showed similar effects of pH on the PLFA pattern, with increasing relative abundance of $16:1\omega 5$, $16:1\omega 7c$, $18:1\omega 7$ and i14:0 as pH increased at this soil depth.

Soil water content is directly related to precipitation, evaporation and movement of groundwater. Overall soil water content decreased with decreasing precipitation. In the arid areas, although a few sites may have been affected by groundwater in the arid areas, the soil water contents remained relatively low where the total biomass was significantly lower than that of the semi-arid areas, indicating that precipitation may still be a main driving force on the surface soil water content. Meanwhile, as precipitation decreased, the potential evaporation was over 50 times higher than MAP in this arid and semi-arid regions (Chen et al. 2006), which could lead to a rapid increase of soil salinity with decreasing precipitation.

Salinity is an important factor affecting cell osmotic pressure (Chowdhury et al. 2011). Soil texture was also linearly correlated with MAP (Figure 2). Soil texture was controlled by a pedogenesis process coupled with biological, chemical and physical weathering. Different climate regions have different soil types. The pedogenesis processes may take thousands, or even millions, of years, depending on the climate region. Thus precipitation, as a climatic factor, may directly influence vegetation, soil water content, soil salinity and even soil texture, and indirectly affect the soil community at different temporal scales.

The size of the microbial biomass and the microbial community structure in the surface soil of the arid, semiarid and Qaidam desert sites was dramatically affected by the change of mean annual precipitation (Figure 4). The clustering of the microbial communities was significantly grouped according to the precipitation gradient, which reflects that precipitation is a main driving force of microbial communities. Interestingly, with decreasing



Fig. 2. Relationships between mean annual precipitation with soil physicochemical characteristics alone the precipitation gradient. (A) total organic carbon (TOC) and total nitrogen (TN); (B) soil moisture and pH; (C) soil texture (clay, silt and sand) content; (D) water extracted chloride, Nitrate and sulfate.



Fig. 3. Total phospholipid fatty acid (PLFA) biomasses for indicator subgroups of bacteria (A), fungi (B) Gram-positive bacteria (C), Gram-negative bacteria (D), and Actinomycetes (E) at 0–5 cm, 5–10 cm, 10–20 cm and 20–40 cm depth soil along the precipitation gradient.

precipitation, the standardized (Z-score) values increased dramatically at the initial stage, and then barely varied (Figures 4A, 4B and 4C), which indicates a nonlinear microbial response to precipitation at different soil depths. Precipitation may function as a main limiting factor for microbial communities in semi-arid and arid ecosystems but may not be a driving force for microbes in the Qiadam desert, where the amount of precipitation is too low. In the semi-arid and arid areas, a change of the microbial community structure was positively related to precipitation, but this positive relationship was weaker in the Qiadam desert area. In the desert area, however, precipitation may not be able to support the microbial community, and the groundwater may play a more important role than precipitation in affecting the microbial community. The soil depth did affect the microbial community structure at every site (Figure 4). In



Fig. 4. First noncanonical axis of the redundancy analysis (RDA) of (A) bacteria at 0-5 cm, (B) bacteria at 5-10 cm, (C) bacteria at 10-20 cm and (D) bacteria at 20-40 cm PLFA profiles versus the standardized (Z-score) values of the annual mean precipitation of each sampling site. The axes explain 33.9%, 42.8%, 33.0% and 23.5% of the variability in the data for bacteria in soil profile at 0-5 cm, 5-10 cm, 10-20 cm and 20-40 cm, respectively.

the arid area, the biomass was concentrated in the deeper soil, with less biomass distributed around the surface.

This distribution may occur because the surface soil microbial community would encounter the challenges of quick evaporation after precipitation events, strong ultraviolet (UV) light with a minimal vegetation canopy and high-amplitude surface soil temperature oscillations. The distribution of bacterial biomass in soil profiles in the semi-arid, arid and Qiadam desert areas also indicates that groundwater has a strong effect on the microbial community. With increasing soil depth, the main driving force for microbes is transformed from precipitation at the 0-5 cm and 5-10 cm soil depths to other forces at the 20–40 cm depth. We speculate that groundwater may pose a significant influence on the 20-40 cm soil depth.

In conclusion, in arid and semi-arid areas of the northeastern Tibetan Plateau, mean annual precipitation was strongly correlated spatially with the soil microbial community, mainly affecting the microbial community in the 0-10 cm soil depth. In the 300–394 mm yr⁻¹ precipitation areas, bacterial biomass was mainly concentrated at the surface, and continued to decrease with increasing soil depth. Therefore, the change of microbial community structure was positive related to precipitation in this area. In the $36-260 \text{ mm yr}^{-1}$ precipitation areas the bacterial biomass was mainly concentrated in the deep soil, and in this area the change of microbial community structure was negatively related to precipitation. The biomasses of Gram-positive bacteria, Gram-negative bacteria and actinomycetes all exhibited the same trend as the total bacteria biomass. Further work is required at both the species and genus level, including the collection and analysis of more soil samples and the inclusion of more environmental factors, to examine taxa details of how the microbial community structure varies biogeographically.

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