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Effects of vegetation type on the microbial characteristics of the fissure soil-plant systems in karst rocky desertification regions of SW China

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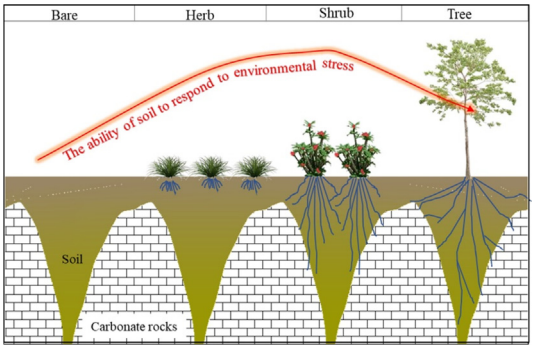
HIGHLIGHTS

- Shrubs could promote soil microbial biomass accumulation better than trees.
- The impact of vegetation types on soil microorganisms was stronger than soil depth.
- Microbes in fissure soil were more sensitive to the environmental factors.

GRAPHICAL ABSTRACT



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ABSTRACT

In karst regions, shallow karst fissure (SKF) soil has proven to be an important plant habitat and soil resource. However, how plants affect the microbial abundance and community composition of SKF soil remains poorly studied. We explored the soil microbial community structure differences in fractured soil-plant systems by determining phospholipid fatty acid (PLFA) profiles under three vegetation types (herbs, shrubs and trees) in SKF and used a bare SKF without vegetation as the control in a karst rocky desertification area. The total microbial biomass and microbial community composition differed between surface soil and SKF soil. The total microbial biomass in surface soil was higher than that in SKF soil. In addition, in contrast to surface soil, the microbial communities in SKF soil were more vulnerable to the effects of environmental variables. Furthermore, plants had a significant positive effect on the accumulation of microbial biomass in surface and SKF soil: shrubs had the strongest effect, followed by trees. Vegetation types significantly affected the ratios of saturated PLFAs to monounsaturated PLFAs (SAT/MONO ratio) and cyclopropyl PLFAs to precursors (cy/pre ratio). In contrast to the SKF without vegetation, the SAT/MONO ratio and cy/pre ratio under grasslands, shrublands and trees were low. Herbs and shrubs had the greatest capacity to enhance the ability of soil to respond to environmental stress compared to trees. Our results suggest that, as an important plant habitat in karst regions, the condition of SKF soil should be urgently improved. The stereoscopic collocation of shrub-grass vegetation may be the preferred measure for vegetation restoration.

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Deep-rooted shrubs and grasses are best at improving soil and plant growth. Our study can be useful for developing strategies for vegetation rehabilitation in karst regions.

1. Introduction

"Stop soil erosion, Save our future" was the theme of World Soil Day 2019 to raise awareness of the importance of soil resources (Food and Agriculture Organization of the United Nations, 2019). Soils have become one of the scarcest natural resources due to the rapid development of the economy and society (Marzaioli et al., 2010; Nabiollahi et al., 2018). Soil erosion is one of the greatest threats to the natural functions and processes of soils (Gonzalez Lago et al., 2019). The soil shortage crisis is the most severe within the fragile natural environments in karst areas. KRD is a type of soil degradation caused by severe soil erosion and occurs in most karst areas, including the European Mediterranean, north and central Vietnam, Java, Indonesia, Kampot Province, southwest Cambodia and southwest China, but the problems caused by KRD are most acute in southwest China (Wang et al., 2004; Kheir et al., 2010; Jiang et al., 2014; Duringer et al., 2012; Stas et al., 2017). Vegetation restoration represents one of the most widely used strategies to reduce soil erosion, and it is also widely practised to control KRD, but the effects are not as beneficial as those in non-karst areas. Due to extended periods of serious soil erosion, the soil in KRD areas has often been badly degraded and is characterized by thinness, insufficient soil water supplies and poor fertility (Fig. 1). The reduction in surface soil resources makes it difficult to support the growth of high-biomass vegetation (Wang et al., 2004). Therefore, solving the problem of soil resource scarcity is the key to promoting the recovery of vegetation in KRD areas.

Many studies have shown that significant quantities of surface soils are leaked or temporarily deposited in SKF as a result of runoff erosion (Wang et al., 2004; Worthington, 2009; Dai et al., 2015). SKF filled with soil form unique and plant-friendly fissured soil habitats similar to flowerpots that feature deep soil layers and high water conditions (Liu, 1993; Yan et al., 2019). These SKF could provide more root space for high-biomass vegetation and become one of the most important habitats in the KRD areas. Because the soil nutrients in SKF are relatively poorer than those in surface soils, it is of fundamental importance to improve soil nutrients and promote soil nutrient cycling for the sustainable utilization of SKF soil resources and vegetation restoration.

Vegetation restoration can not only be used to restore the functioning of damaged ecosystems but also influence belowground soil microbial community properties (Morriën et al., 2017). Soil microorganisms are a major component of terrestrial ecosystems and participate in the biogeochemical cycling of soil nutrients by acting as decomposers or mutualists (Dantas and Sommer, 2014; Tedersoo et al., 2014). The significance of soil microbiomes with plants has been closely investigated globally. Previous work has shown that the litter and secretions of plants are important carbon sources for soil microorganisms. Plant root exudates could promote the development of soil microbes in root environments. Similarly, increasing attention has focused on the significance of the role of soil microbiomes in degraded karst ecosystems. Key environmental factors, such as vegetation succession (Zhao et al., 2019), soil pH (Qi et al., 2018), soil particulate organic matter chemistry (Xiao et al., 2017), soil CO_2 (Coleborn et al., 2016), and rhizosphere exudates (Pan et al., 2016), have often been used to highlight the differences in microbial communities between karst areas and non-karst areas (Fan et al., 2019). The current research has adequately revealed the relationship between plants and soil microorganisms. Numerous studies have focused exclusively on the top 20 cm or less of soil because the average surface soil layer is <30 cm in karst areas. Nevertheless, the soil depth from the surface to a SKF is often >100 cm. Hartmann et al. (2009) demonstrated that the total microbial biomass of the soil layer below 20 cm is approximately 35%. Moreover, there are differences in the soil conditions and distributions of plant roots and litter between the surface and SKF. Therefore, the impact of the plants on soil microorganisms in a SKF is bound to exhibit differences. Furthermore, both surface soil and SKF soil suffer from hydraulic erosion, while the hydrological processes of surface soil and fissured soils are different. This difference may result in different sensitivities of microorganisms to the environmental factors in surface and fissured soils (Peng and Wang, 2012; Fu et al., 2016). In contrast, little is known about how soil microbiomes from surface to SKF soil and soil properties respond to the vegetation types of karst ecosystems, especially in SKF soil profiles.

The aims of this study were i) to gain insight into the vertical distribution patterns of the soil microbial community compositions from the surface to SKF soil and ii) to reveal the effects of vegetation types on soil microbial community compositions. We explored differences in the soil microbial community structures in a fissure soil-plant system under three vegetation types (herbs, shrubs and trees) in a SKF by determining phospholipid fatty acid (PLFA) profiles, and a bare SKF without vegetation was used as the control in the KRD area. Our study could provide an integrated perspective on development strategies that could be used for vegetation restoration in karst regions in southwest China and would also be applicable to fragile karst ecosystems in other areas around the world.

Fig. 1. Karst rocky desertification landscape in a degraded karst area of southwestern China.

2. Materials and methods

2.1. Study sites

We sampled 20 sites located in Anshun city, Guizhou Province in the southwest karst area of China (26°7′8″N, 105°49′45″E, Fig. 2). The region is identified as a subtropical monsoon climate with the major soil type designated as calcareous soil according to the China Soil Classification system. The mean thickness of the surface soil layer is 20 cm. The highest annual average temperature is 22.4 °C, while the lowest average is 3.8 °C, the average annual temperature is 21.7 °C, and the average annual rainfall is 1193 mm. Before 2003, the study sites were slope farmland. Slope land has often suffered severe soil erosion and land degradation due to improper long-term cultivation techniques that have aggravated the fragile ecological environment. Therefore, the Chinese government began to perform vegetation restoration projects in this area after 2003. The main vegetation types in this area are annual herbs (*Setaria viridis* (L.) Beauv, *Bidens pilosa* L and *Sonchus oleraceus* L.), perennial herbs (*Imperata cylindrica* (L.) Beauv, *Miscanthus floridulus (Lab.) Warb. ex Schum et Laut* and *Cynodon dactylon* (Linn.) Pers), shrubs (*Rosa cymosa* Tratt., *Pyracantha fortuneana* (Maxim.) Li, *Rosa roxburghii* Tratt. f. normalis Rehd.et Wils. and *Coriaria nepalensis Wall*), and trees (*Toona sinensis* (A. Juss.) Roem, *Itea chinensis Hook.* et Arn and Roem. *Robinia pseudoacacia Linn*).

2.2. Soil sampling & soil properties

In July 2018, we selected 5 sample sites (50 × 50 m) featuring representative structures and vegetation for each vegetation type (Table 1). The vegetation types growing above the SKF included herbs (HF), shrubs (SF) and trees (TF), while the SKF (BF) without growing plants were regarded as the control group. The distance between any two sample sites was <100 m to reduce the impact of habitat heterogeneity on soil microorganisms. Then, a sub-plot (20 × 20 m) with similar environmental conditions was selected in each site (Fig. 3a). Three replicates SKFs were selected in each sub-plot. We determined the position and edge of the SKF by judging the depth of the drill rod inserted into the soil (Fig. 3b). Five surface soil samples (0–20 cm, S) were taken and mixed as one soil composite sample (three replications). The fissure soil sampling depths were 30–50 cm (F1), 50–70 cm (F2) and 70–90 cm (F3) (Fig. 3c). Because the total amount of soil inside a fissure is relatively small, we collected all the soil samples from each layer with a small shovel and then removed plant debris from the soil samples and sieved the soil through a 2-mm sieve. Three replicates of mixed soil samples for each layer were selected to determine the soil properties. Each soil sample was subdivided into two parts, and the samples were used for i) the determination of soil physicochemical properties (air-dried indoors), ii) analysis of soil PLFA profiles (during field sampling, the samples were stored at 4 °C in a portable icebox. In the laboratory, the samples were stored at −80 °C until analyses).

Table 1
General situation of study sites.

Fracture type	BF	HF	SF	TF
Slope/°	17–23	16–24	16–25	17–23
Vegetation type	Bare land	Herb	Shrub	Tree
Bedrock	Limestone	Limestone	Limestone	Limestone
Soil type	Limestone soils	Limestone soils	Limestone soils	Limestone soils
Surface soil thickness/cm	24–28	23–29	26–29	25–30
Fissure length/cm	93–112	96–116	92–118	94–112

Note:BF, HF, SF and TF are bare land, herb, shrub and tree, respectively.

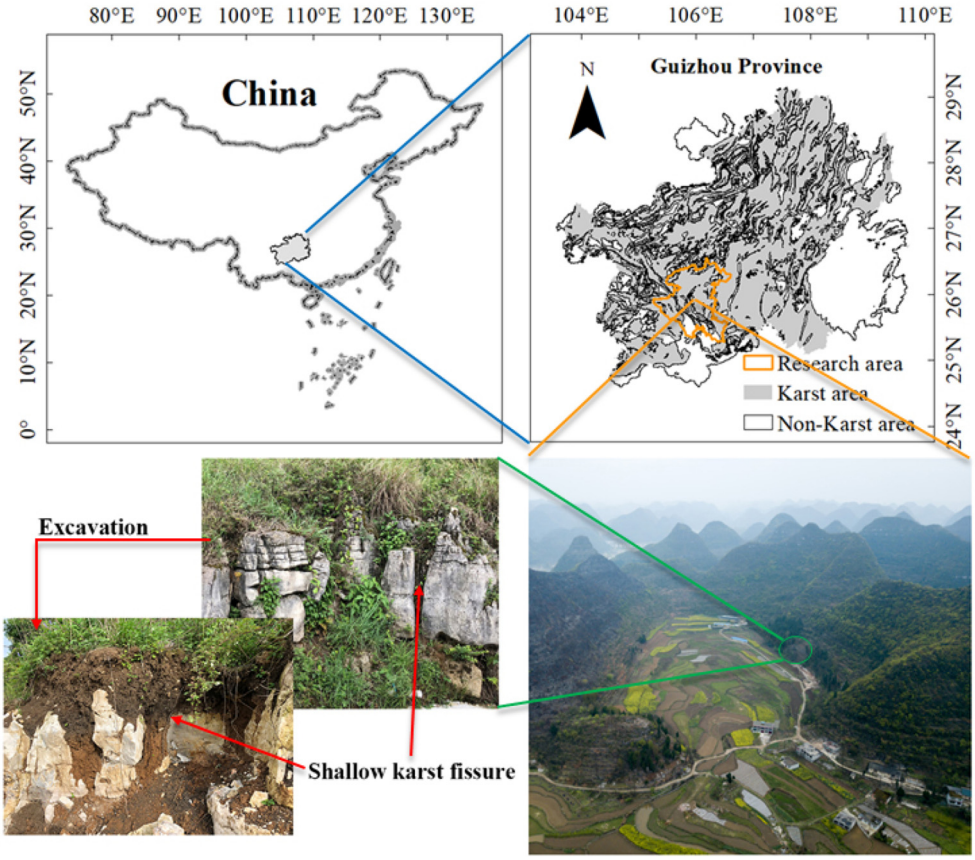

Fig. 2. Geological map of the study area and sampling area.

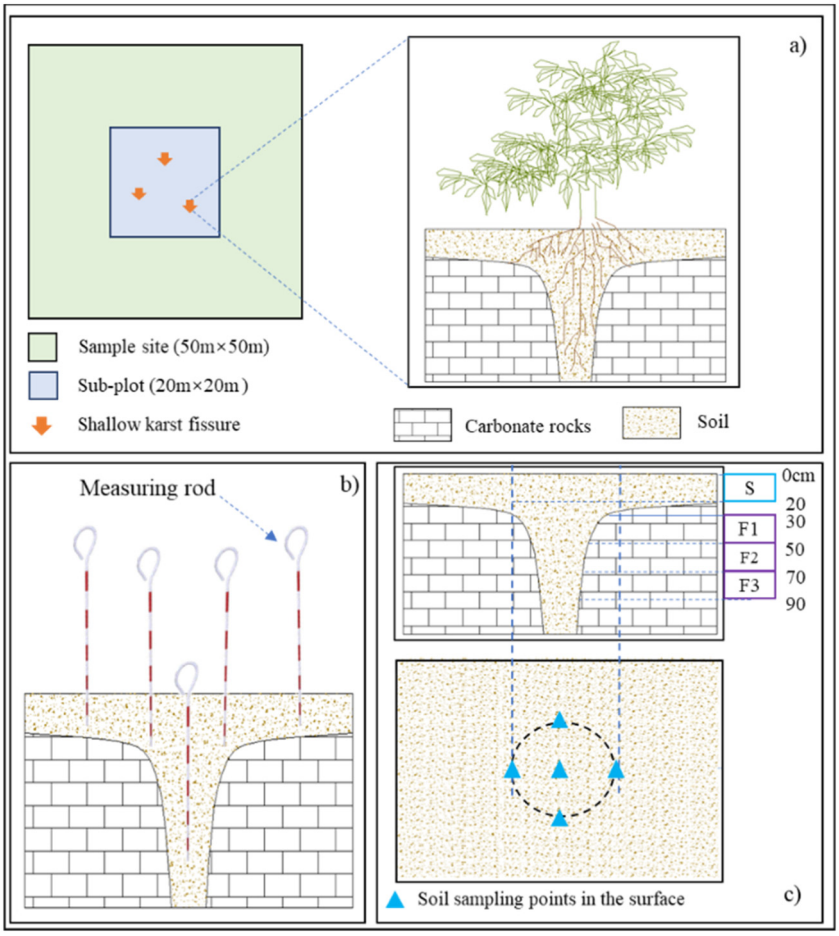

Fig. 3. Diagrammatic sketch of soil sampling Note: a) Schematic diagram of the sampling sites, b) chain pin method for determining the location of fractures, c) diagrammatic sketch of soil sampling position. S, surface soil; F1, F2 and F3 are soil samples with depths of 30–50, 50–70, and 70–90 cm in shallow karst fissure, respectively. BF, bare land; HF, herb; SF, shrub; TF, tree. The same below.

Soil pH was measured in 1:5 (v/v) soil: distilled H_2O extracts. Soil organic carbon (SOC) and organic matter (OM) were determined by the potassium dichromate oxidation heating method (Kalembasa and Jenkinson, 1973). Total nitrogen (TN) was analysed by using an automatic Kjeldahl apparatus (Jackson, 1959). C/N ratio (ratio of SOC to TN).

2.3. PLFA analysis

The microbial community structure was measured by PLFA analysis based on the modified procedures of Frostegård et al. (1993), which were further described by Pollierer et al. (2015). The relative abundance of each PLFA ($n \cdot mol\ g^{-1}$ soil, dry weight) was calculated to represent the community composition. The sum of all biomarkers was used as a proxy for the total microbial biomass (total PLFAs). The selected PLFAs included i13:0, a13:0, i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, i18:0 and i19:0 to represent gram-positive bacteria (GP), while PLFA biomarkers 14:1 w5c, 16:1 w7c, 17:1 w8c, 18:1 w7c, cy17:0 and cy19:0 were grouped as gram-negative bacteria (GN). Bacterial biomass ($PLFA_{bact}$) was the sum of GP and GN (Frostegård and Bååth, 1996; Zelles, 1999). Fungal PLFAs ($PLFA_{fungi}$) were quantified as the sum of 16:1 w5c, 18:1 w9c and 18:1 w5c (Frostegård and Bååth, 1996; Zelles, 1999; Bååth and Anderson, 2003). Actinomycete PLFAs ($PLFA_{act}$) were determined according to 16:0 10 Mel, 17:0 10 Mel and 18:0 10 Mel (Zelles, 1999). PLFA 20:4 w6c and 20:1 w9c were used as the protozoan biomarkers ($PLFA_{pro}$) (Doran et al., 2007). F/B ratio (ratio of fungal to bacterial biomass) and stress indicators [cy/pre ratio (ratio of cyclopropyl PLFAs (cy17:0+ cy19:0) to precursors PLFAs (16:1 w7c+18:1 w7c), SAT/MONO ratio (ratio of saturated PLFAs to monounsaturated PLFAs)] (Moore-Kucera and Dick, 2008; Trögl et al., 2015).

2.4. Statistical analysis

Statistical analysis was performed using SPSS 19.0 (IBM Inc. NC, USA), and significant differences in total microbial biomass, F/B ratio, cy/pre ratios and SAT/MONO ratios were determine by repeated measures general linear models (GLMs). STATISTICA 12.5 (StatSoft Inc. Tulsa, USA) was used to analyse the differences in PLFA composition (logit-transformed mole percentage values) by discriminant function analysis (DFA). Redundancy analysis (RDA) were conducted in Canoco 5 (Microcomputer Power, Ithaca, NC, USA).

3. Results

3.1. Soil chemistry characteristics

As shown in Fig. 4, the OM and TN of the surface and SKF soil exhibited significant differences between vegetation types (GLM, $F_{3,\ 273} = 6.12$, $P = .0005$ and $F_{3,\ 273} = 4.82$, $p = .0027$ for OM and TN, respectively) and soil layers (GLM, $F_{3,\ 273} = 29.52$, $P = .0000$ and $F_{3,\ 273} = 17.13$, $p = .0000$ for OM and TN, respectively). As the vegetation in the fissure changed from herbs to trees, the OM and TN showed increasing trends. In addition, the OM and TN gradually and significantly decreased with increasing soil depth, which were significantly lower in the SKF than at the surface (Tukey test, $P < .05$), but the OM and TN of the SKF did not differ significantly among the different soil depths

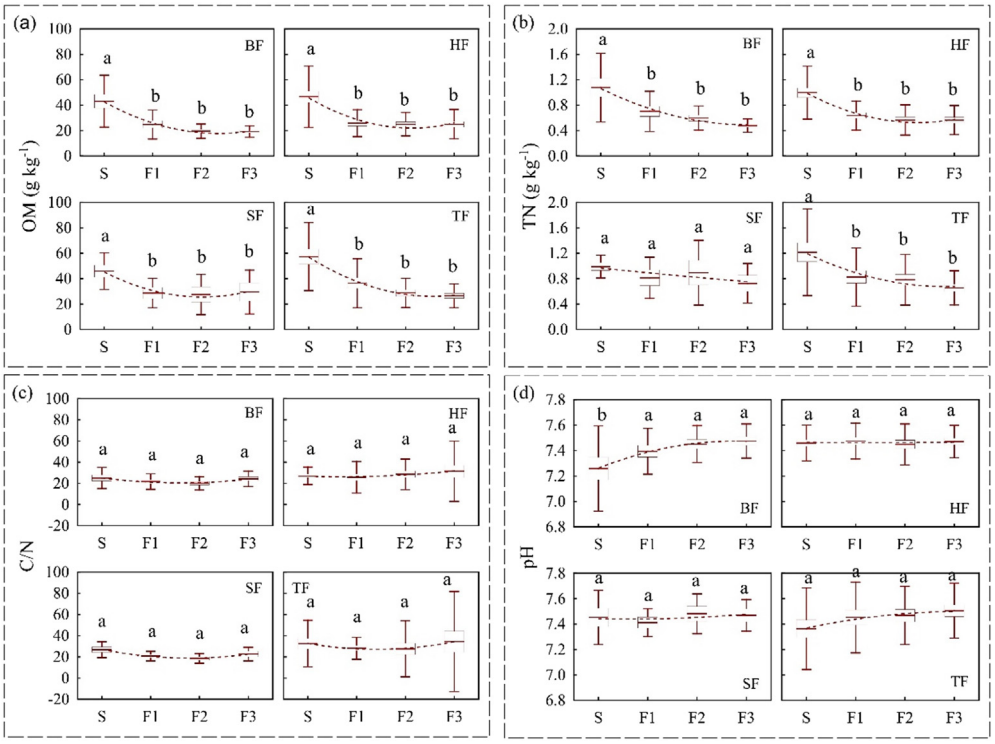

Fig. 4. Soil chemistry characteristics in different soil depth and vegetation type. Note: OM, soil organic matter; TN, total nitrogen; C/N, ratio of soil organic carbon to total nitrogen. Different lowercase letters indicate significant difference under soil depths ($P < .05$), different uppercase letters indicate among different vegetation types at the same depth ($P < .05$). The same below.

(Tukey test, $P > .05$). The C/N ratio and pH did not differ significantly (Tukey test, $P > .05$) between vegetation types (GLM, $F_{3,\ 273} = 2.50$, $P = .0597$ and $F_{3,\ 273} = 1.55$, $p = .2013$ for the C/N ratio and pH, respectively) and soil layers (GLM, $F_{3,\ 273} = 0.78$, $P = .5081$ and $F_{3,\ 273} = 2.46$, $p = .6318$ for the C/N ratio and pH, respectively). In contrast, the soil fertility of the SKF was markedly poorer than that of the surface. Furthermore, the soil fertility levels of the surface and SKF soil were generally arranged as BF < HF < SF < TF.

3.2. Soil microbial biomass

A total of 25 kinds of PLFAs were detected in the surface and SKF soil, including 17 species of bacteria, 3 species of fungi, 3 species of actinomycetes and 2 species of protozoa (Fig. 5). The PLFAs of the surface and SKF soil were mainly composed of 16:1w7c, 18:1w7c, cy19, i15:0, i16:0, 16:1w5c, 18:1w9c, 10Mel 16:0 and 10Mel 18:0. The total abundances of these PLFAs accounted for 64% to 75% of the total PLFA abundance. The PLFA composition of the surface and SKF soil were presented as bacteria (62.07% ± 4.16%) > fungi (19.61% ± 4.16%) > actinomycetes (15.65% ± 4.11%) > protozoa (2.67% ± 0.71%).

The difference in the total amount of PLFAs between the surface and SKF was due to the comprehensive effect of vegetation type and soil depth ($F_{9,\ 32} = 2.47$, $P = .0288$, repeated measures GLM within-subject effect for vegetation type × soil depth, Fig. 6). Vegetation types had a large influence on the total amount of PLFAs compared to the soil depth (GLM, $F_{3,\ 32} = 4.34$, $P = .0112$ and $F_{3,\ 32} = 2.35$, $P = .0908$

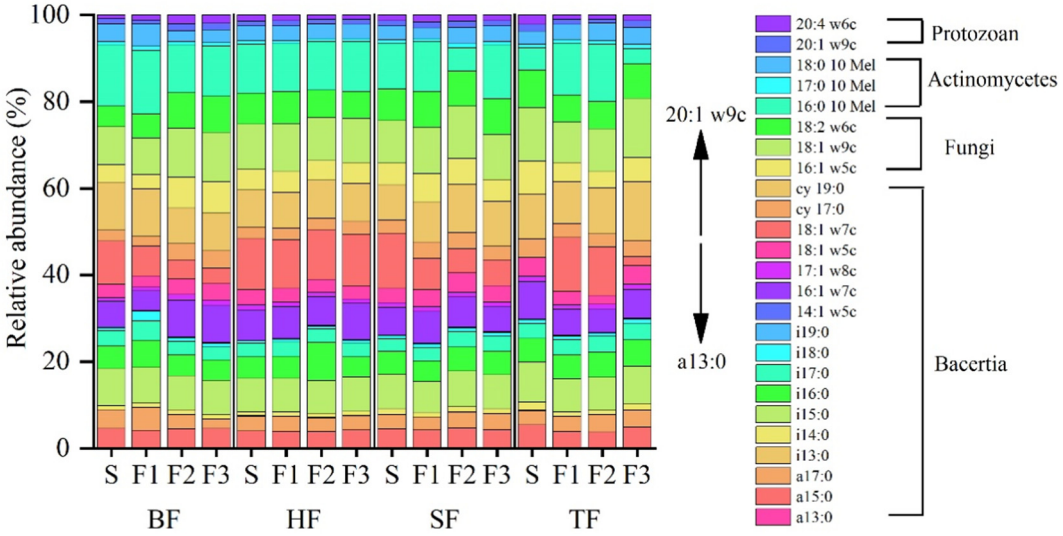

Fig. 5. Soil microbial composition in different soil depth and vegetation type.

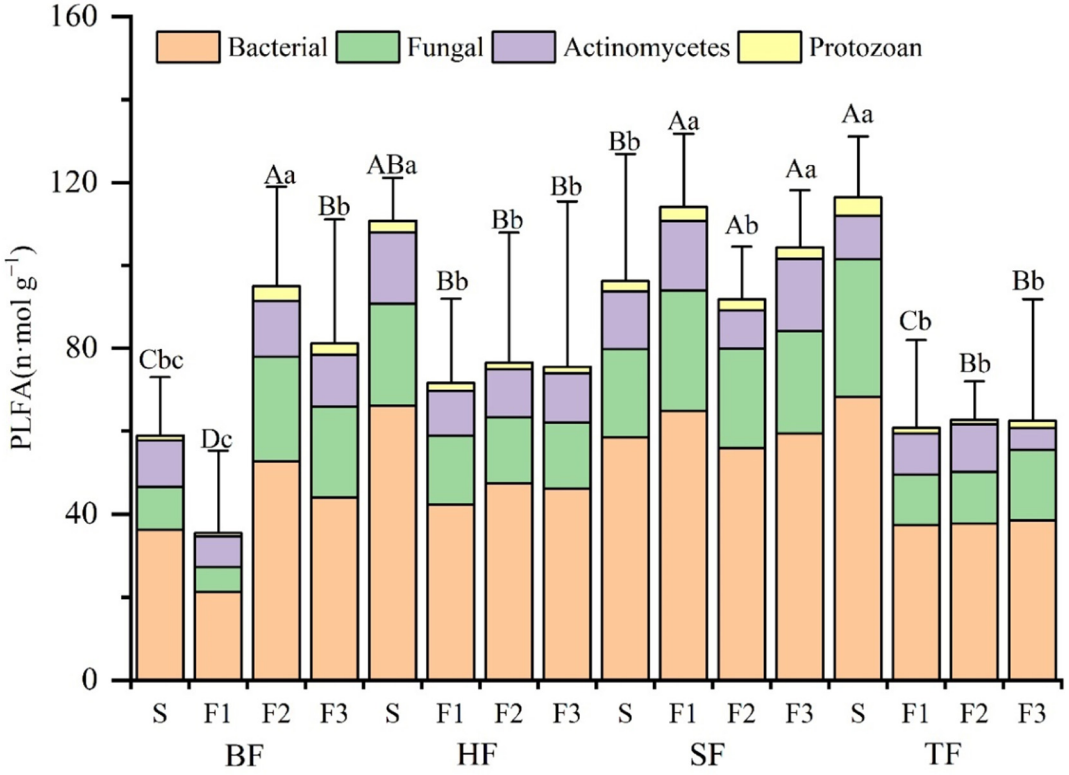

Fig. 6. Microbial composition and biomass (total PLFAs) in different soil depth and vegetation type.

for vegetation type and soil depth, respectively). The total amount of PLFAs between each soil layer differed under the various vegetation types. The vertical change in the total amount of PLFAs from the surface soil (S layer) to the F3 layer of the SKF soil showed a V-shaped change and a minimum in the F1 layer of the SKF soil. The total amount of PLFAs in the surface soil (92.29 ± 26.34 nmol·g^{-1}) was significantly higher (Tukey test, $P < .05$) than that in the SKF (69.54 ± 30.23, 78.39 ± 22.39, 77.76 ± 29.75 for F1, F2 and F3, respectively).

The total amount of PLFAs showed significant differences between each vegetation type (DFA, $F_{75, 60} = 8.17$, $P < .0000$, Fig. 6). The total amount of PLFAs was significantly affected by vegetation type (GLM, $F_{3, 32} = 4.34$, $P = .0112$). The total amount of PLFAs in SF soil (97.64 ± 17.52 nmol·g^{-1}) was significantly (Tukey test, $P < .05$) higher than that under the other vegetation types (66.78 ± 26.93 and 72.78 ± 29.03 nmol·g^{-1} for BF and TF, respectively) but not HF (Tukey test, $P > .05$, 80.78 ± 28.72 nmol·g^{-1}).

3.3. Soil microbial community composition

The PLFA composition significantly differed between the surface and SKF soil and within the SKF soil ($F_{75, 60} = 12.638$, $p < .0000$; DFA, Fig. 7a, Table 2). The furthest squared Mahalanobis distance was between F1 and F3 (54.11, $P < .0001$), and the shortest squared Mahalanobis distance was between F2 and F3 (7.33, $P < .0001$). The first axis and second axis of the DFA separated each soil layer. The difference was mainly due to different proportions of the bacteria PLFAs i15:0, 14:1w5c, 16:1w7c, and cy 17:0 and fungal marker 16:1w5c and actinomycete marker 17:0 10Mel (for Pearson correlations, see Table 3).

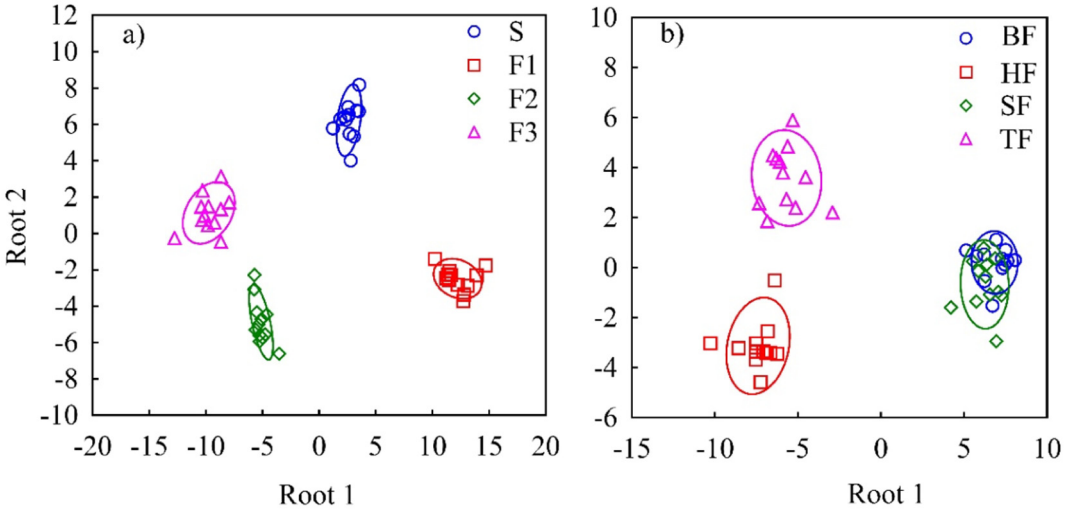

Fig. 7. Discriminant function analysis of the PLFA composition of soil in different soil depth and vegetation type. Note: Ellipses represent confidence intervals at $P < .05$.

Table 2
Squared Mahalanobis distances between group centroids and reliability of discrimination for PLFA composition of soil in different vegetation types and soil depth.**

Type	BF	HF	SF	S	F1	F2
HF	23.74***	–	–	–	–	–
SF	2.32*	21.70***	–	–	–	–
TF	19.05***	5.28***	17.94***	–	–	–
F1	–	–	–	18.77***	–	–
F2	–	–	–	20.06***	34.09***	–
F3	–	–	–	20.35***	54.11***	7.33***

*** $P < .001$.
** $P < .01$.
* $P < .05$.

The PLFA composition of soils was significantly different between each vegetation type ($F_{75, 60} = 8.137$, $p < .0000$; DFA, Fig. 7b, Table 2). The furthest squared Mahalanobis distance was between BF and HF (23.74, $P < .0001$), and the shortest squared Mahalanobis distance was between BF and SF (2.32, $P < .05$). The first axis of the DFA separated BF and SF from the other vegetation types. Differences were mainly due to differing proportions of the bacteria PLFAs a13:0, i13:0, 14:1w9c, a15:0, i17:0, 17:1w8c, i18:0, and i19:0 and the fungal PLFA 16:1w5c (for Pearson correlations, see Table 4).

The impacts of vegetation types and soil layers on the F/B ratio are the result of a comprehensive role. The F/B ratio of soil did not significantly differ between vegetation types or surface and SKF soil, whereas the F/B ratio of soil was significantly affected by the combined effect of vegetation type and soil layer ($F_{9,32} = 4.952$, $P < .01$, repeated measures GLM within-subject effect for vegetation type × soil depth). The F/B ratio in the S layer was higher (0.33 ± 0.04) than that in the F2 layer (0.32 ± 0.08) and F1 layer (0.30 ± 0.07) (Fig. 8a). Moreover, the F/B ratio was the highest in SF (0.35 ± 0.03) and decreased in the order TF (0.32 ± 0.04) > BF (0.31 ± 0.08) > HF (0.30 ± 0.03) (Fig. 8b). The stress indicator SAT/MONO ratio and cy/pre ratio did not differ significantly between soil layers, whereas they differed significantly between vegetation types ($F_{3,32} = 3.240$, $P < .05$ and $F_{3,32} = 4.344$, $P < .05$ for SAT/MONO ratio and cy/pre ratio, respectively; repeated measures GLM between-subject effects for vegetation types, Fig. 8d,f). The stress indicator SAT/MONO ratio and cy/pre ratio were both significantly lower in the soil of HF than in the soil of the other vegetation types (Tukey test, $P > .05$). The SAT/MONO ratio of the soil in HF was 0.54 ± 0.08 and increased in the order SF (0.62 ± 0.17) < TF (0.67 ± 0.09) < BF (0.73 ± 0.28). Similarly, the cy/pre ratio increased in the order TF (1.30 ± 0.63) > BF (1.14 ± 0.65) > SF (1.04 ± 0.47) > HF (0.66 ± 0.18).

Table 3
Pearson correlations between single significant PLFAs of soil and the first two axes of the DFA discriminating between soil layers.

Index	Root1	P	Root2	P
a 13:0	−0.03	**	0.08	**
cy 17:0	−0.01		0.04	**
a 15:0	−0.01	*	0.08	**
i 19:0	−0.02	*	0.03	**
i 15:0	−0.01		0.08	***
17:1 w8c	−0.02	*	0.06	***
18:1 w9c	−0.02		0.05	***
14:1 w5c	−0.01		0.05	***
a17:0	0.00	*	0.06	***
i 20:0 i	−0.02		−0.01	***
20:1 w9c	−0.01	*	0.06	***
17:0 10 Mel	−0.01		0.06	***
16:1 w5c	−0.01	**	0.04	***
i 17:0	−0.01	**	0.05	***
18:1 w7c	0.01	**	0.02	***
i 16:0	−0.02	*	0.02	***
18:0 10 Mel	−0.02	*	0.08	***
16:0 10 Mel	0.00	*	0.02	***
18:1 w5c	−0.01		0.05	***
cy 19:0	−0.02	*	0.05	***
20:4 w6c	−0.01	**	0.05	***
i 18:0	0.00	***	0.01	***
i 14:0	−0.01	*	0.09	***
16:1 w7c	−0.01		0.05	***
i13:0	0.00		0.08	***

*** $P < .001$.
** $P < .01$.
* $P < .05$.

Table 4
Pearson correlations between single significant PLFAs of soil and the first two axes of the DFA discriminating between vegetation types.

Index	Axis1	P	Axis2	P
18:1 w7c	−0.024	**	−0.199	**
19:0 cy	0.010	*	0.030	***
i20:0	0.058	**	−0.015	***
18:1 w9c	0.003	**	−0.022	***
20:4 w6c	0.022	**	0.015	***
i16:0	−0.014	*	−0.077	***
16:1 w7c	0.001		−0.048	***
17:0 cy	0.020	**	0.038	***
16:1 w5c	0.021	**	0.000	***
17:0 10 Mel	0.008	**	−0.026	***
i18:0	0.048		0.059	***
i17:0	0.007		−0.028	***
14:1 w9c	0.009		0.023	***
a15:0	0.016		−0.007	***
i14:0	0.002	**	0.067	***
i15:0	0.005	**	−0.028	***
18:0 10 Mel	0.001		−0.060	***
14:1 w5c	−0.004	*	−0.043	***
16:0 10 Mel	0.028	**	−0.156	***
20:1 w9c	0.022		−0.003	***
18:1 w5c	0.021		−0.022	***
i13:0	0.000		−0.033	***
17:1 w8c	0.012		−0.018	***
a13:0	−0.002		0.025	***
i19:0	0.032		−0.036	***

*** $P < .001$.
** $P < .01$.
* $P < .05$.

3.4. Microbial community composition as influenced by soil depth and vegetation type

The results of RDA of the soil microbial community structure between the surface and SKF soil, with pH, TN and SOC as supplementary variables, separated the surface soil from SKF soil along the first axis and separated F1 from F2 and F3 (Fig. 9a). The second axis also separated the surface soil from SKF soil and separated F3 from F1 and F2. The first axis was closely related to SOC, while the second axis was associated with TN. PCAs of the relative abundances of individual PLFAs also separated the surface soil from SKF soil, with SOC (explaining 59.2% of the variation), TN (explaining 12.5% of the variation) and pH (explaining 28.3% of the variation) contributing to the separation, but SOC and TN were negatively related to pH. The concentrations of the PLFAs i14:0, i15:0, a15:0, i16:0, a17:0, 18:1w7c, and 20:4w6c were highest in soils with high SOC and TN. In contrast, a13:0, i13:0, i17:0, i18:0, i19:0, 14:1 w5c, 14:1 w9c, 20:1w9c, cy17:0, cy19:0 and 17:0 10Mel were highest at high pH values.

RDA of the relative abundance of individual PLFAs confirmed the differences in the soil microbial community structure under different vegetation types and separated the BF and TF from SF and HF along the first axis (Fig. 9b). The first axis was closely related to TN. The second axis separated the BF and HF from SF and TF and was associated with SOC.

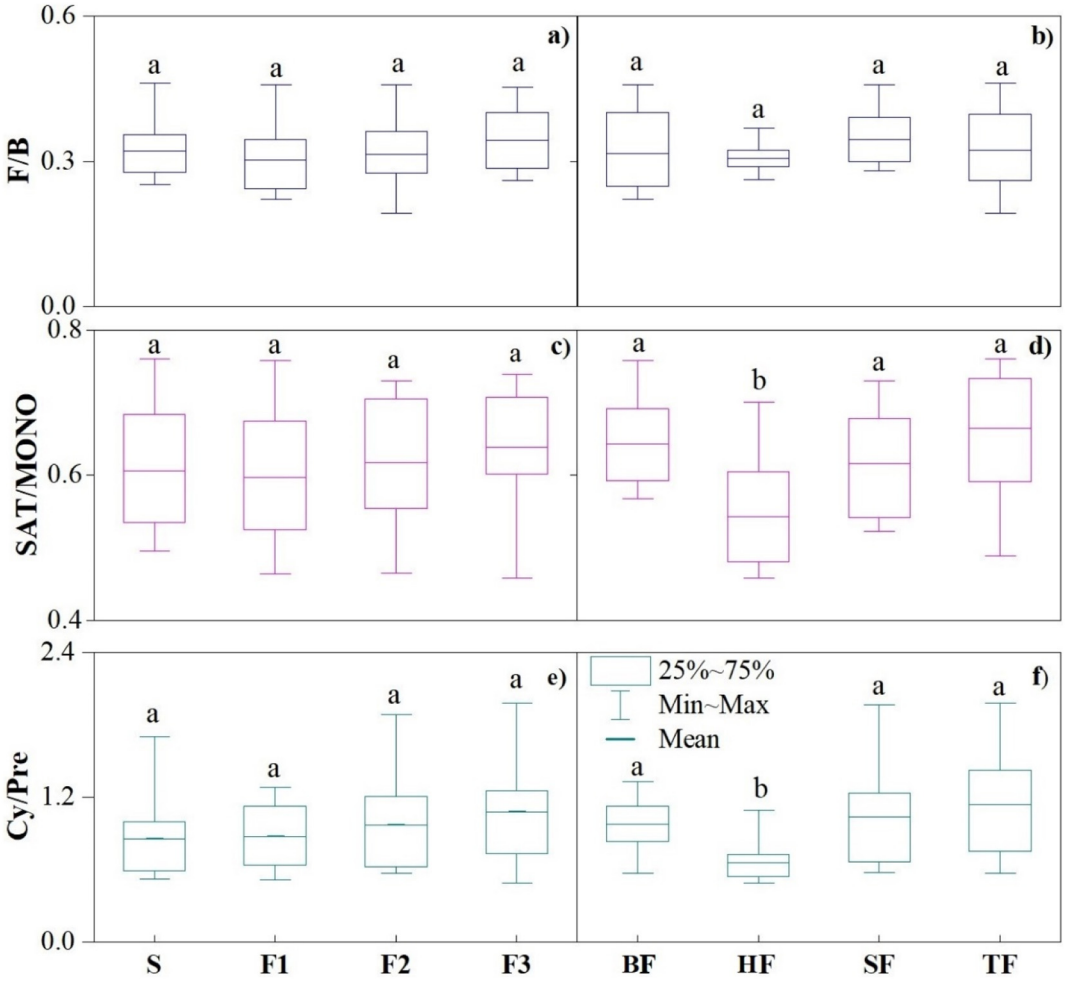

Fig. 8. Microbial ratio and stress indicators in different soil depth and vegetation type.

In addition, SOC, TN and pH also contributed to the separate relative abundances of individual PLFAs between each vegetation type. SOC separated BF from HF, SF and TF. TN separated TF from BF, HF and SF. pH separated SF from BF, HF and TF. Concentrations of PLFAs a13:0, i13:0, i18:0, i19:0, 14:1 w5c, 14:1w9c, 17:1 w8c, 17:0 10 Mel, were higher at higher SOC values. The concentrations of PLFAs i14:0, 16:1w5c, cy17:0, a15:0, cy19:0, 18:1w5c, i16:0, 18:0 10 Mel, i15:0, a17:0, i17:0, and 18:1 w9c were positively correlated with TN and pH.

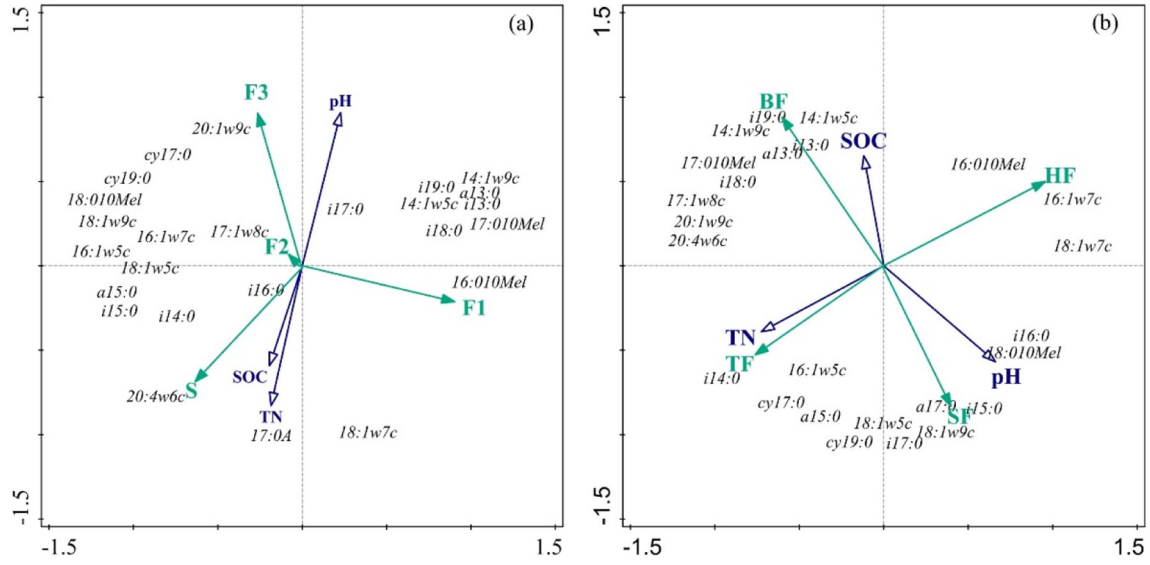

Fig. 9. Redundancy analysis of the relative abundance of individual PLFAs in different soil depth and vegetation type with pH, TN and SOC as supplementary variables.

4. Discussion

4.1. Effect of vegetation type on surface and SKF soil microbial biomass

Plants can affect the soil microbial characteristics, but the effect reduces as the soil depth increases. The results of this study showed that plants have a positive effect on the microbial biomass of surface and SKF soil. In contrast to the total amount of PLFAs in the fissures (BF) without growing plants, the total amounts of PLFAs in surface and SKF soil in HF, SF and TF were higher, especially in the S and F1 layers. Due to the thin surface soil layer (≤30 cm) along with its low fertility, surface soil is not conducive to plant growth (Zhang et al., 2018). The hydrotropism and gravitropism of plant roots causes them to extend into fissure soils to absorb more water and nutrients for growth (Nie et al., 2019). Meanwhile, the intercalation, rhizosphere effect and exudates of roots improve soil properties and provide soil microbes with nutrients (Bigott et al., 2019), contributing to the accumulation of microbial biomass in the soil. Previous studies reported that the microbial biomass increased with succession in the order grass < shrub < trees (Liu et al., 2015; Zhao et al., 2019). This pattern was not observed in our study, and the total amount of PLFAs decreased in the order SF > HF > TF > BF (Fig. 10). The difference was due to the fact that previous studies considered only the effect of vegetation on the surface soil. In fact, surface soil and SKF soil should be considered a single unit to comprehensively evaluate the effects of plants on the soil in KRD areas. The taproots of trees are highly developed and affect deep soils. Shrubs and herbs have dense lateral roots, and this dense fibrous root network allows more soil to be subjected to the physiological and biochemical effects of the root system (Walton et al., 2000; Chok et al., 2004). In addition, SKF provide the main channel for runoff infiltration, and the soil in SKF is highly susceptible to underground leakage driven by runoff. Compared with trees, the root networks of shrubs and herbs have a better fixing effect on the surface soil and more effectively reduce runoff infiltration, thus reducing the effect of hydraulic erosion on fissured soil; soil microorganisms therefore suffer relatively low erosion in response (Preston and Crozier, 1999).

Furthermore, the total amount of PLFAs in surface soil was significantly higher than that in SKF soil. This result may have been caused by two factors. Plant litter decomposes into soil nutrients and provides an important source of microbial nutrition and energy (Angst et al., 2019). Additionally, plant root density decreases with the increase in soil depth, which causes the activation of roots in surface soil to be more effective than that in SKF soil, with this effect decreasing with increasing soil depth (Hicks Pries et al., 2018). Additionally, a previous study found that soil erosion intensity is inversely proportional to soil microbial biomass (Hu et al., 2019). The migration and redistribution of soil nutrients caused by soil erosion-sedimentation is an important cause of the difference in the soil microbial biomass distribution in eroded areas (Onet et al., 2019). The dual hydrological structure of karst slopes causes the surface and fissured soil to simultaneously suffer from hydraulic erosion (Worthington, 2009). Nutrients in the surface and fissured soils migrate due to runoff, resulting in differences in the soil microbial biomass distribution. Stored-full runoff was previously found to be the main runoff yield pattern over karst slopes (Chai, 1989). Most rainfall reaches the surface and infiltrates into the soil, entering cenotes through the SKF. During these hydrological processes, soil particles are eroded by runoff, and runoff dissolves and carries soil nutrients, which results in the nutrient contents of fissured soil decreasing with the increase in soil depth (Song et al., 2017). The results indicated that herbs, shrubs and trees all enrich the accumulation of soil microbial biomass, and being the significant potent was shrubs.

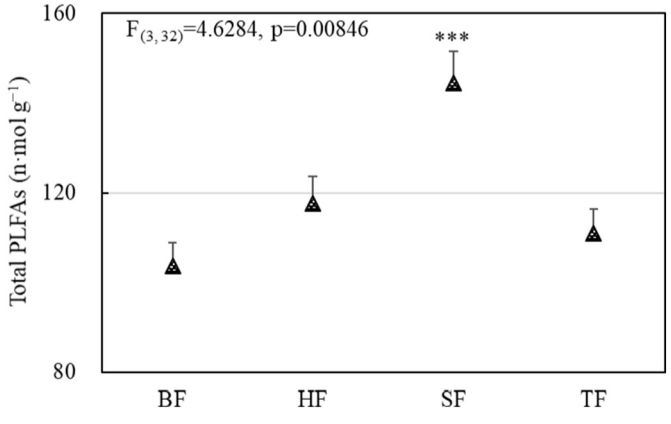

Fig. 10. Characteristics of the total amount of PLFAs under the various vegetation types. Note: *** represent confidence intervals at $P < .001$.

4.2. Effect of vegetation type on surface and SKF soil microbial community composition

The PLFA composition of surface soil was separated from SKF soil, mainly due to different proportions of some bacterial PLFAs, the fungal marker 16:1w5c, and the actinomycete marker 17:0 10Mel, suggesting differences in the compositions of bacterial, fungal and actinomycete communities. The ratio of PLFA markers can express the soil quality and its ability to respond to environmental stresses. The SAT/MONO ratio and cy/pre were lower at the surface than those in the SKF soil, but these differences were not as pronounced as of the differences in the cy/pre ratio, suggesting that the cy/pre ratio is a more sensitive stress indicator in the investigated systems (Thiet et al., 2006; Huang et al., 2009; Trögl et al., 2015). High F/B ratios indicate that the soil ecosystem is stable (Knivett and Cullen, 1965; Zhao et al., 2012; Xu et al., 2014). While the F/B ratio of soils was generally high in the surface soil, the stress indicators for the surface soil were lower than those in the SKF soil, suggesting that SKF soil is more susceptible to stress (Ananyeva et al., 2015; Dickens et al., 2015). Compared to surface soil, SKF soil is exposed to more hydrological processes, suggesting that the microbial community in SKF soil is exposed to more serious soil erosion than the surface soil. This result suggests that the disturbances and fluctuations in environmental conditions are more pronounced in SKF soil than in surface soil due to the effects of the vegetation root systems and hydraulic erosion.

In addition, the SAT/MONO ratio and cy/pre ratio were lowest in HF and generally increased in the order SF < TF < BF (see Section 3.3: Soil microbial community composition). Moreover, the F/B ratio was the highest in SF and decreased in the order TF > BF > HF. The stress indicators of HF, SF and TF were lower than that in BF, and the F/B ratio in the soil (HF, SF and TF) with plants was generally higher than that in BF without plants, suggesting that plants could alleviate the stress on the microbial community in surface and SKF soil. Furthermore, the results indicated that soil in HF and SF has stronger resistance to environmental pressure than TF, and the soil ecosystem is more stable in SF than that under other vegetation types. The roots of herbs form a dense, impervious layer on the surface soil, which can effectively protect the surface soil from soil erosion, but its effect on the improvement of deep soil is poor. The aboveground parts of shrubs can effectively reduce soil erosion, and the root system network can also effectively improve soil properties (Burylo et al., 2011). Although the aboveground biomass of trees is large and the root distribution is deep, the protective effects of trees on the surface soil are weaker than those of herbs and shrubs. In addition, the deep root systems of trees are mainly taproots and are otherwise sparsely distributed (Yurkevich, 2012; Broedel et al., 2017). Therefore, the improvement of soil by tree roots is relatively weaker than the improvement by shrubs. Based on vegetation restoration and soil erosion control, stereoscopic collocation of shrub-grass vegetation is the preferred measure for improving soil properties, accumulating microbial biomass and cycling nutrients.

5. Conclusions

Plants have demonstrated a beneficial effect in improving the nutrient contents and microbial biomass in the surface and SKF soil of KRD slopes. The nutrients and microbial biomass in grasslands, shrublands and forests were significantly higher than those in the SKF without plants. Soil microbial biomass accumulation was significantly affected by the plant type. In contrast to our initial assumption, soil microbial biomass in shrublands was higher than that in grasslands and forests. This result suggests that shrubs are better at promoting microbial biomass accumulation in both surface and fissured soils. In addition, microbial communities in surface and SKF soil differ in susceptibility to stress, and our results show that the stress indicators (ratio of SAT/MONO and cy/pre) of SKF soil were lower than those of surface soil, while the F/B ratio was also lower, suggesting that the microbial communities in SKF soil were more sensitive to changes in environmental variables and may suffer more serious hydraulic erosion. Furthermore, the SAT/MONO ratio and cy/pre were lowest in HF, followed by SF, and the F/B ratio was the highest in SF. This finding suggests that herbs and shrubs more effectively enhance the ability of soil to respond to environmental stress and that shrubs can better maintain the stability of the soil ecosystem. We concluded that the stereoscopic collocation of shrub-grass vegetation can be a preferred strategy for vegetation restoration, and deep-rooting plants are more favourable for vegetation growth and improvement of soil microorganisms and ecological quality in SKF habitats.

Declaration of competing interest

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

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