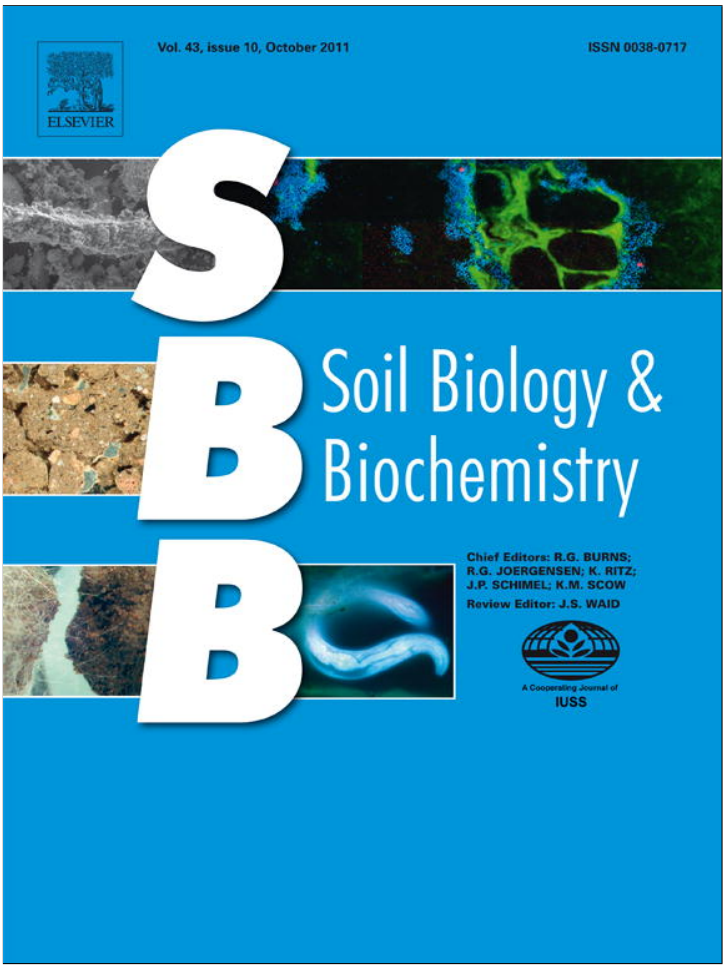

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Soil microbial community changes and their linkages with ecosystem carbon exchange under asymmetrically diurnal warming

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ABSTRACT

The greater increase in daily minimum temperature than daily maximum temperature has been widely observed at global scale. A growing body of evidence suggests that this asymmetrically diurnal warming has great impacts on aboveground ecological processes. However, little is known about the effect of the asymmetrically diurnal warming on belowground biotic organisms. This study was conducted as part of a field manipulative experiment with day (6:00 a.m.–6:00 p.m.), night (6:00 p.m.–6:00 a.m.) and diurnal warming (24 h) in a temperate steppe, to assess shifts in soil microbial community composition and physiology in response to asymmetrically diurnal warming. Our results show that contrasting hydro-thermal conditions of the two experimental years (2006–2007) reshaped microbial community structure and modified C use patterns in the grassland ecosystem. Consistent with our hypothesis, day and night warming had different effects on some specific microbial groups and microbial C utilization potential. Significant reductions in the relative proportion of total bacteria, gram-positive bacteria and arbuscular mycorrhizal fungi and microbial C utilization potential, were observed under conditions of night warming only. The close association of microbial C utilization patterns with ecosystem C exchange and coupled responses of plant and microbe to night warming highlight physiological continuity in plant–microbe–soil system.

1. Introduction

Climate warming resulting from anthropogenic activities features spatial difference and temporal asymmetry (Kerr, 2007; IPCC, 2001, 2007). Asymmetrically diurnal warming with greater increase in daily minimum temperature than that in daily maximum temperature has been observed in different regions across the globe (Karl et al., 1991; Easterling et al., 1997, 2000; Rebetez, 2001; IPCC, 2001; Alexander et al., 2006). The effects of asymmetric day and night warming on terrestrial ecosystem structure and functioning have been well documented. However, most of the previous studies were focused on aboveground vegetation and ecological processes (Alward et al., 1999; Peng et al., 2004; Volder et al., 2004; Volder et al., 2007; Zhou et al., 2007; Beier et al., 2008; Wan et al., 2009; Xia et al., 2009). To the best of our knowledge, few studies have been conducted to evaluate the effect of asymmetrically diurnal warming on belowground microorganisms and soil C processes mediated by microorganisms. Elucidation of responses of microbial community composition and physiology to the climate change will improve the prediction of ecosystem-climate feedbacks.

Climate warming may induce variations in soil microclimates (Wan et al., 2002; Xia et al., 2009). This in turn can have great effects on soil microbial community composition and physiology (Zogg et al., 1997; Drenovsky et al., 2004; Papatheodorou et al., 2004; Delippe et al., 2005; Zhang et al., 2005; William and Rice, 2007; Chen et al., 2007). Shifts in microbial community are likely to be induced by variability in plant parameters as well, since microbes and plants are interdependent with each other (Högberg and Read, 2006). Given the different impacts of day and night warming on hydro-thermal factors (Xia et al., 2009) and plant physiology (Wan et al., 2009), it is reasonable to expect that day and night warming may differentially affect microbial composition and/or physiology.

Griffiths et al. (2004) proposed that stabilization in microbial-mediated functions in a system is closely related to soil microbial

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composition. Microbial communities with greater diversity are more resistant or resilient to environmental changes. Shifts in microbial composition may be accompanied with physiological shifts under asymmetrically diurnal warming. Furthermore, changes in microbial community composition and physiological processes have well been documented to modify ecosystem processes due to their important role in terrestrial ecosystems (Gallo et al., 2004; Putten, 2005; Malcolm et al., 2009; Compant et al., 2010). Increasing evidence demonstrates that microbial community physiology links to ecosystem C and N cycling and balance (Melillo et al., 2002; Schimel et al., 2005; Schimel et al., 2007). Therefore, responses of microbial community composition and physiology may contribute to ecosystem C exchange in the context of asymmetrically diurnal warming.

To test the responses of microbial community composition and physiology to asymmetrically diurnal warming, a field experiment including the control, day (6:00 a.m.–6:00 p.m., local time), night warming (6:00 p.m.–6:00 a.m.) and diurnal warming (24 h) was established in a semiarid grassland ecosystem in April 2006. This grassland ecosystem has been shown to be sensitive to climate warming (Gong et al., 2004; Piao et al., 2003; Niu et al. 2008; Yang et al., 2011). Previous studies conducted in the same area have revealed that night warming induced greater increase in daily mean soil temperature and lower reduction in soil moisture than day warming did (Wan et al., 2009; Xia et al., 2009). Furthermore, responses of plant photosynthesis, soil respiration and gross ecosystem productivity to day warming differ from night warming (Wan et al., 2009; Xia et al., 2009). Therefore, it is reasonable to expect that day and night warming may impose asymmetric effects on soil microbial communities, since microbial growth and activities are sensitive to soil microclimates and closely associated with plants.

2. Materials and methods

2.1. Site description and experimental design

The manipulative experiment was carried out in a semiarid temperate steppe located in Duolun County of Inner Mongolia, China (42°.02′ N, 116°.17′ E, 1324 a.s.l.), where the mean annual air temperature is 2.1 °C, with the minimum temperature in January (−17.5 °C) and maximum temperature in July (18.9 °C). The mean annual precipitation (1953–2007) is 383 mm with about 86% occurring from May to September. The soil is classified as Haplic Calcisols in the FAO classification, with $62.75 \pm 0.04\%$ sand, $20.30 \pm 0.01\%$ silt, and $16.95 \pm 0.01\%$ clay. The mean soil bulk density is 1.31 g cm^{-3} and pH is 6.84 ± 0.07. The dominant plant species include *Stipa krylovii*, *Artemisia frigida*, *Potentilla acaulis*, *Cleistogenes squarrosa*, *Allium bidentatum*, *and Agropyron cristatum.*

The study was conducted as part of a field experiment with a complete random block design. Thirty six 3×4 m^2 plots were established, and 3 m distance was kept between two adjacent plots. Six treatments, control (C), day warming (D, 6:00 a.m.–6:00 p.m.), night warming (N, 6:00 p.m.–6:00 a.m.), diurnal warming (W, 24 h), nitrogen addition, and nitrogen addition plus diurnal warming, were conducted with 6 replicates per treatment. One MSR-2420 infrared heater (165 cm × 15 cm; Kalglo Electronics Inc., Bethlehem, PA, USA) was suspended overhead 2.5 m above the ground in each of the warmed plots since April 2006. In order to simulate the shading effects of the heater, a 'dummy' heater with the same size as the infrared heater was installed in each control plot.

2.2. Soil sampling and measurements

Two soil cores (8 cm in diameter and 15 cm in depth) were collected from each plot and completely mixed into one composite fresh soil sample in August 2006 and 2007, respectively. After sieving out plant roots and stones with 2 mm mesh, soil samples were packed in ice blocks and stored at 4 °C, and transported to laboratory within 24 h for further measurements. Hydro-thermal parameters and microbial community composition were measured using all 6 replicates per treatment, while microbial C utilization patterns were determined using 3 samples randomly chosen from the 6 replicates per treatment.

Soil temperature (ST) at 10 cm depth was automatically recorded with a Datalogger (STM-01 Soil Temperature Measurement System, Henan Electronic Institute, Zhengzhou, China). Daily maximum, minimum and hourly mean temperatures in soils were measured. Soil moisture content (SM) at 10 cm depth was recorded biweekly with a portable soil moisture probe (Diviner 2000, Sentek Pty Ltd, Balmain, Australia).

Microbial C utilization patterns were measured by the community-level BIOLOG assay within 24 h after soil sampling. Compared with the traditional culture-based taxonomic approach, the Biolog assay is a simple and rapid method to characterize the physiology of heterotrophic microbial communities, although it only reflects the catabolic potentials and can't detect slow-growing microbial activities (Garland and Mills, 1991; Preston-Mafham et al., 2002). EcoPlates were used to determine C utilization potential of active and fast-growing bacteria. Carbon substrates in EcoPlates were assigned as amines, amino acids, carbohydrates, carboxylic acids, polymers, phenolic compounds and root exudates, as reported by Insam (1997). Further analysis was performed with the protocols described by Classen et al. (2003). Samples of composite fresh soil (4 g) were extracted with 36 ml of 50 mM K_2HPO_4 buffer (pH = 6), and then shaken on a reciprocal shaker for 30 min. After settling for 30 min, soil suspensions were obtained and diluted 1:1000 with sterile inoculating solution (0.40% NaCl and 0.03% Pluronic F-68 in deionized water) for bacterial incubation. Bacterial inoculations were accomplished by transferring 150 μl solution to each of the 96 wells in each EcoPlate. All plates were placed in polyethylene bags to minimize desiccation during incubation. EcoPlates were incubated at 25 °C for 96 h, and read at 595 nm at intervals of 24 h. All solutions, equipments and glassware were sterilized in advance with an autoclave. Preliminary assay showed fungal detection after 72 h, and thus the optical density readings at 72 h were used to analyze bacterial C utilization patterns. The optical density value per well was corrected by the reading of water control in each plate. The negative values or those values less than 0.06 were adjusted to zero due to the detection limits of system (Miguel et al., 2007). Average well-color development (AWCD) which reflects microbial activities was determined for each EcoPlate, according to Garland and Mills (1991) as follows:

$$\mathrm{AWCD} = \sum_{i=1}^{n} (x_i - c)/31,$$

where x_i is the optical density value measured at 595 nm in substrate i, and c is the value measured in the control well.

Phospholipids fatty acid (PLFA) analysis was used to evaluate microbial community composition. The chemotaxonomic method is one of the most common approaches. This method avoids the requirement for cultivation and enables the analysis of nearly 99% of natural populations, including those unculturable populations (Amann et al., 1995). In brief, PLFA was extracted from a fresh soil equivalent to 8 g dry weight, and then fractionated and quantified following protocols described by Bossio and Scow (1998). Extracted fatty acid methylesters were identified with a standard qualitative mix ranged from C9 to C30 and MIDI peak identification system (Microbial ID. Inc., Newark, DE). 'A:BωC' was used as the nomenclature for fatty acid, as reported by Bossio and Scow (1998). The

relative biomass of bacteria was estimated by the summed concentration of the following fatty acids i15:0, a15:0, 15:0, i16:0, a17:0, i17:0, cy17:0, 17:0 and cy19:0 (Frostegård et al., 1993; Frostegård & Bååth, 1996; Zak et al., 1996), while fungal biomass was determined by 18:1ω9, 18:2ω6 and 18:3ω6 (Federle, 1986; Frostegård & Bååth, 1996; Zak et al., 1996; Zogg et al., 1997). The branched PLFAs i15:0, a15:0, i16:0, a17:0, i17:0 were chosen as indicators of gram-positive bacteria (GP, Zak et al., 1996; Bardgett et al., 1996; Frostegård & Bååth, 1996; Zogg et al., 1997; Ringelberg et al., 1997). cy17:0 and cy19:0 were used as biomarkers for gram-negative bacteria (GN, Zak et al., 1996; Zogg et al., 1997). Fatty acid 16:1ω5c can be assigned as a biomarker for arbuscular mycorrhizal fungi (AMF, Olsson et al., 1995), although it has also been found in some bacteria (Frostegård et al., 1993; Zak et al., 1996).

2.3. Data analysis

Software R was used to perform all statistical analyses. Soil hydro-thermal factors and microbial parameters were analyzed by repeated measures ANOVA, where between- and within-subject variations in year and treatments were determined. Interannual variability in soil microbial community composition and C utilization patterns were assessed by multi-response permutation procedures (MRPP). Partial redundancy analysis (Partial RDA) in vegan package of R (Oksanen et al., 2007) was carried out to test the effects of day or night warming on microbial community. In the partial RDA model factors were coded into binary dummy variable matrix and then, one of these matrices was used as covariate matrix to test the effect of the others (Legendre and Legendre, 1998). A permutation test was performed to make a statistical inference of correlations of microbial C use patterns with hydro-thermal factors and ecosystem C exchange. The constrained matrix of SM, ST, GEP, SR and ER was standardized using the function decostand before permutation test was carried out. Cor.test was used to detect relationships between microbial parameters and hydro-thermal factors.

3. Results

3.1. Soil microclimates

Compared with long-term mean annual precipitation (MAP, 383 mm) from 1953 to 2007, a wetter year (6.5% greater annual precipitation than MAP) and a drier year (44.4% lower annual precipitation than MAP) were observed in 2006 and 2007, respectively. However, there was a wetter August in 2007 with 5.85 w/w% (absolute value) higher SM and 2.05 °C lower ST than those in 2006 (Fig. 1 and Table 1). Across the 2 years, night warming caused greater increment in ST than day warming did (Fig. 1 and Table 1). However, slight reductions in SM under day and night warming were found, although they were not statistically significant (Fig. 1 and Table 1).

3.2. Interannual differences in soil microbial community composition and C utilization patterns

Soil microbial community composition in 2006 was significantly different from that in 2007 ($P < 0.001$, MRPP pairwise comparison). The mole percentage PLFA of bacteria, gram-positive bacteria, fungi and the ratio of gram-negative to gram-positive bacteria (GN/GP) were interannually different (Fig. 2 and Table 1). The ratio of cy17:0 to ω7-precursor varied with year as well ($P < 0.001$, repeated measures ANOVA). The relative proportion of bacteria, gram-positive bacteria and fungi was greater in wetter August 2007 than in 2006 (Fig. 1). However, the ratios of cy17:0 to ω7-precursor

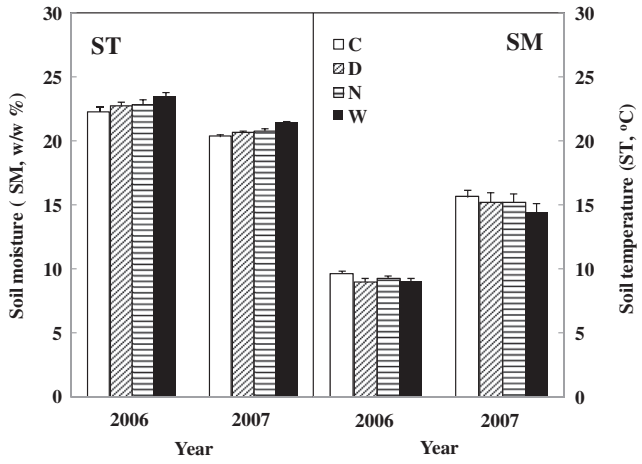

Fig. 1. Soil moisture and temperature under day, night and diurnal warming (Mean ± S.E., $N = 6$). ST, soil temperature; SM, soil moisture.

and gram-negative to gram-positive bacteria in 2007 were lower than those in 2006.

Significant interannual differences in microbial C utilization patterns were observed ($P < 0.001$, MRPP pairwise comparison) with 85% greater AWCD in 2007 than that in 2006 (Table 2). Except phenolic compounds, the uses of other six C source types in the 2 years were different (Fig. 3 and Table 2). Stronger use potentials of the six C source types by bacteria were found in 2007 rather than 2006 (Fig. 3). Moreover, the interannual differences in the use potentials of all C source types were disproportionally greater under diurnal warming than day and night warming (Fig. 3).

3.3. Effects of asymmetrically diurnal warming on microbial community composition and C utilization patterns

Neither day nor night warming altered soil microbial community structure in the steppe (both $P > 0.05$, Partial RDA), although night warming dramatically affected some specific microbial groups. Night warming decreased the mole percentage PLFAs of total bacteria, gram-positive bacteria and arbuscular mycorrhizal fungi across the 2 years (Fig. 2 and Table 1). In addition, marginal decreases in the mole percentages of gram-negative bacteria and fungi occurred under night warming during the 2 years (Fig. 2 and Table 1).

Night warming significantly affected microbial C utilization patterns in the semiarid steppe ($P = 0.026$, Partial RDA), while day warming did not ($P > 0.05$, Partial RDA). Across the 2 years, night warming caused a great reduction in AWCD (Fig. 3 and Table 2). Night warming also interacted with day warming to affect AWCD (Table 2). Similarly, night warming had negative impacts on the use potentials of amines, amino acids and polymers, and marginally reduced the utilization of root exudates (Fig. 3 and Table 2). Significant interactions between day and night warming in affecting the uses of amines, amino acids and root exudates were observed as well (Table 2).

3.4. Associations of microbial communities with soil microclimate and ecosystem C exchange

Across the experimental period, the mole percent PLFAs of total bacteria ($\text{cor} = -0.54$, $P < 0.0001$), gram-positive bacteria ($\text{cor} = -0.52$, $P < 0.001$) and fungi ($\text{cor} = -0.55$, $P < 0.0001$) were negatively correlated with ST. In contrast, GN/GP ($\text{cor} = 0.36$, $P = 0.012$) and the ratio of cy17:0 to ω7-precursor ($\text{cor} = 0.44$, $P = 0.002$) positively depended upon ST in both years. Close

Table 1
Results (P value) of repeated measures ANOVA on the effects of day and night warming on soil microclimates and the mole percentage PLFA of the main microbial groups. SM, soil moisture; ST, soil temperature; B, bacterial PLFA; GN, gram-negative bacterial PLFA; GP, gram-positive bacterial PLFA; F, fungal PLFA; AMF, arbuscular mycorrhizal fungal PLFA; GN/GP, the ratio of gram-negative to gram-positive bacterial PLFA; F/B, the ratio of fungal to bacterial PLFA. The degrees of freedom (d.f.) for the numerator are shown in the table. The denominator d.f. is 40.

Source of variance	Soil properties			Microbial properties						
	d.f.	SM	ST	B	GN	GP	AMF	F	GN/GP	F/B
Year (Y)	1	<0.001	<0.001	0.005	0.468	0.011	0.147	0.003	0.005	0.080
Day warming (D)	1	0.162	0.026	0.974	0.829	0.824	0.468	0.817	0.906	0.477
Night warming (N)	1	0.320	0.009	0.036	0.079	0.025	0.017	0.056	0.965	0.418
D × N	1	0.997	0.693	0.575	0.685	0.380	0.890	0.603	0.634	0.657
D × Y	1	0.753	0.729	0.601	0.963	0.574	0.880	0.819	0.663	0.253
N × Y	1	0.470	0.918	0.625	0.087	0.684	0.656	0.675	0.470	0.168
D × N × Y	1	0.562	0.586	0.598	0.541	0.920	0.756	0.588	0.567	0.583

correlation between AMF and ST was also detected (cor = −0.38, $P = 0.010$). There was no relationship between microbial groups and SM (all $P > 0.05$). AWCD was negatively correlated with ST (Fig. 4a), and positively correlated with SM over the 2 years (Fig. 4b). ST ($r^2 = 0.43$, $P = 0.004$) and SM ($r^2 = 0.59$, $P < 0.001$) accounted for the variability in soil microbial C utilization patterns (Fig. 5). In addition, soil microbial C utilization patterns showed strong associations with soil respiration (SR, $r^2 = 0.48$, $P = 0.001$), gross ecosystem productivity (GEP, $r^2 = 0.44$, $P = 0.002$) and ecosystem respiration (ER, $r^2 = 0.60$, $P < 0.001$) (Fig. 5).

4. Discussions

4.1. Interannual changes

A growing body of evidence suggests that hydro-thermal factors play critical roles in regulating not only aboveground vegetation but also belowground organisms, especially in dryland ecosystems (Weltzin et al., 2003; Zavaleta et al., 2003; Christensen et al., 2004; Yang et al., 2011). This study provides explicit evidence that both microbial composition and their physiology were largely responsive to interannual variability in hydro-thermal conditions in the semiarid grassland. Cycloprophyl fatty acid with stable structure can usually minimize membrane lipid loss and acclimatize drought-stress compared to their monoenoic precursors and saturated branched-chain fatty acid (Iyyemperumal and Shi, 2007; William and Rice, 2007). Greater ratios of cycloprophyl fatty acid (cy17:0)/monoenoic precursor and GN/GP resulting from drier environment in August 2006 indirectly indicate the important role of soil water availability in triggering interannual shifts in microbial community composition. In addition, our findings that microbial C utilization potential in wetter August 2007 was greater than that in drier August 2006 indicate that water availability played a key role in controlling microbial physiological activities.

Under diurnal warming, disproportional differences in microbial use potentials of nearly all C source types between the two years with contrasting hydro-thermal conditions suggest that interannual shifts in microbial physiology may change with treatment (Fig. 3). The indirect effects of warming via altering plant growth may be a possible explanation for this result. There was an increase in soil available nitrogen under diurnal warming in 2007, but not in 2006 (Xia et al., personal communication). The increased soil N availability may stimulate plant growth. In fact, gross ecosystem productivity (GEP) and ecosystem respiration (ER) in August 2007 were 2.4-fold and 1.2-fold greater than those in August 2006 under diurnal warming, respectively. These differences were much higher than interannual differences under day or night warming. It is expected that the stimulation of plant production would modify the effects of diurnal warming on microbial C utilization potential by regulating root exudation in the rhizosphere.

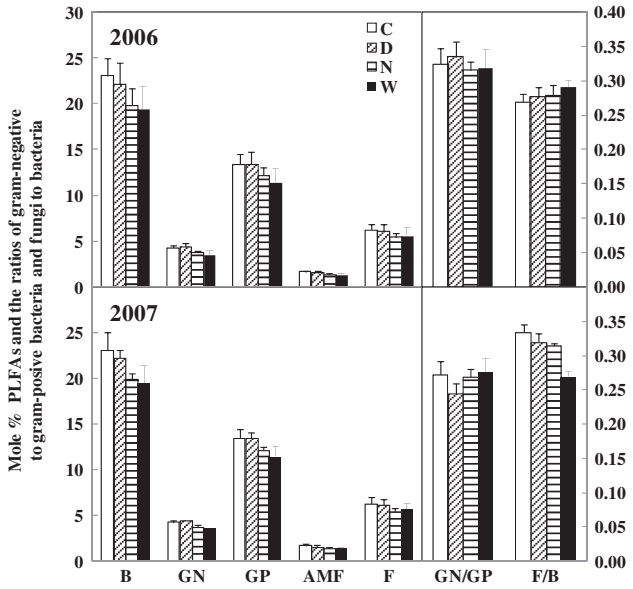

Fig. 2. The mole percentage PLFA (mol %) of main microbial groups and their ratios under day, night and diurnal warming (Mean ± S.E., $N = 6$). B, bacterial PLFA; GN, gram-negative bacterial PLFA; GP, gram-positive bacterial PLFA; AMF, arbuscular mycorrhizal fungal PLFA; F, fungal PLFA; GN/GP, the ratio of gram-negative to gram-positive bacterial PLFA; F/B, the ratio of fungal to bacterial PLFA.

4.2. Warming effects

Non-significant changes in the whole patterns of microbial composition indicate that day and night warming may not be able to restructure microbial communities by changing environmental and/or plant properties in the ecosystem. Consistent with our observations, resistance of microbial composition to experimental warming in the short term was reported in a subarctic health (Rinnan et al., 2007). However, the findings that specific microbial groups and C utilization potential dramatically responded to day or night warming provide experimental evidence that day and night warming can affect microbial communities differently. Variations in total bacteria, GP and AMF mirrored microbial C utilization potential under night warming, which supports the hypothesis that there are close links of microbial groups to their physiological traits (Kourtev et al., 2002, Griffiths et al., 2004). Shifts in hydro-thermal factors can partly account for the negative impacts of night warming on several microbial groups and microbial C utilization potential, but could not explain the absence of day or diurnal warming effects. Overcompensation of plant photosynthesis and

Table 2
Results (*P* value) of repeated measures ANOVA on the effects of day and night warming on average well-color development (AWCD) and the uses of different C source types. The degrees of freedom (d.f.) for the numerator are shown in the table. The denominator d.f. is 16.

Source of variance	d.f.	Amines	Amino acids	Carbohydrates	Carboxylic acids	Polymers	Phenolic compounds	Root exudates	AWCD
Year (Y)	1	0.045	0.006	0.017	0.002	0.001	0.250	0.011	0.012
Day warming (D)	1	0.013	0.183	0.236	0.776	0.970	0.541	0.359	0.341
Night warming (N)	1	0.037	0.029	0.178	0.109	0.042	0.965	0.075	0.062
D × N	1	<0.001	0.001	0.178	0.057	0.068	0.195	0.005	0.023
D × Y	1	0.065	0.559	0.413	0.511	0.201	0.153	0.495	0.650
N × Y	1	0.883	0.623	0.452	0.112	0.819	0.422	0.572	0.421
D × N × Y	1	0.156	0.070	0.185	0.169	0.193	0.100	0.069	0.089

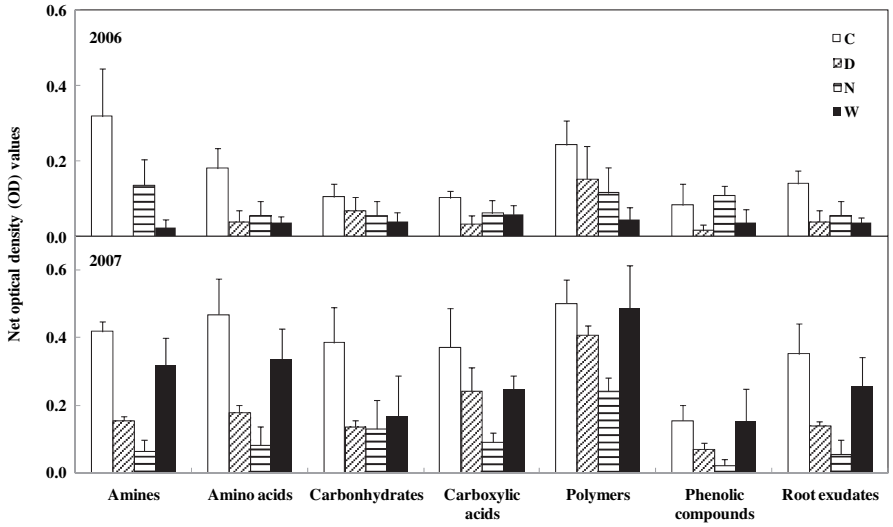

Fig. 3. The potential uses of different C source types under day, night and diurnal warming in both 2006 and 2007. C, control; D, day warming; N, night warming; W, diurnal warming.

consequent net C assimilation increase were observed (Xia et al., 2009; Wan et al., 2009). Greater plant C assimilation may provide more energy for microbial growth and activities, which could help to interpret microbial responses under night warming exclusively.

Large reductions in bacterial C utilization potential under night warming can be primarily attributed to the drop of amino compound use potentials. As the preferentially used substrates by bacteria (Csonka, 1989), amino compounds contain the main soluble organic N in soils and can be directly taken up by plants (Kaye and Hart, 1997; Bardgett et al., 2003). Nitrogen limitations to plants and microbes have been documented in the ecosystem (Zhang et al., 2008; Bai et al., 2010). Furthermore, night warming stimulated soil respiration and gross ecosystem productivity in the same experiment, while day or diurnal warming had no effect (see Table 1 and Fig. 1 in Xia et al., 2009). The enhanced C assimilation implies stimulation of N uptake (Reich et al., 2006; Sokolov et al., 2008), suggesting intensified competition for N between plants and microbes (Kaye and Hart, 1997; Bardgett et al., 2003). This may account for decline in microbial C utilization potential under night warming. In addition, suppression of AMF under night warming may aggravate the competition between plants and soil microbes, because AMF, as widespread plant symbionts, can facilitate plant N uptake (Torpy et al., 1999; Sullivan et al., 2006; Bunn et al., 2009; Van Der Heijden et al., 2008).

4.3. Associations of soil microbial C utilization patterns with ecosystem C exchange

Physiological costs imposed by microorganisms can induce shifts in ecosystem C and N allocation and cycling (Grayston et al., 2001; Zak et al., 2003; Balser and Firestone, 2005; Cookson et al., 2007; Schimel et al., 2007; Reed et al., 2010). Better understanding of microbial ecology can help improve the prediction of climate-ecosystem feedbacks. In this study, close correlations of microbial physiology with gross ecosystem productivity, ecosystem respiration and soil respiration and their coupled responses to warming treatments (see Table 1, Fig. 1 and Fig. 3 in Xia et al., 2009 and Fig. 1a in Wan et al., 2009) provide a tangible evidence for tight linkages of organism-level to ecosystem-level C processes. Högberg and Read (2006) argued that C release from living plant roots, plant symbionts and other rhizosphere soil microbes is, to a large extent, driven by recent plant photosynthesis. Overcompensation of plant photosynthesis and consequent increase in plant C assimilation induced by night warming observed in the same experiment (Wan

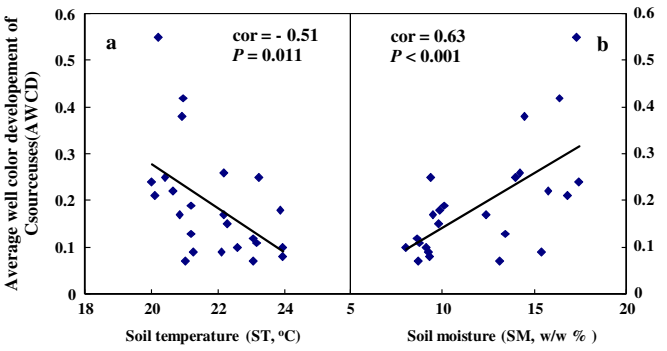

Fig. 4. Correlations of average well-color development (AWCD) with (a) soil temperature and (b) soil moisture at 0–10 cm depth.

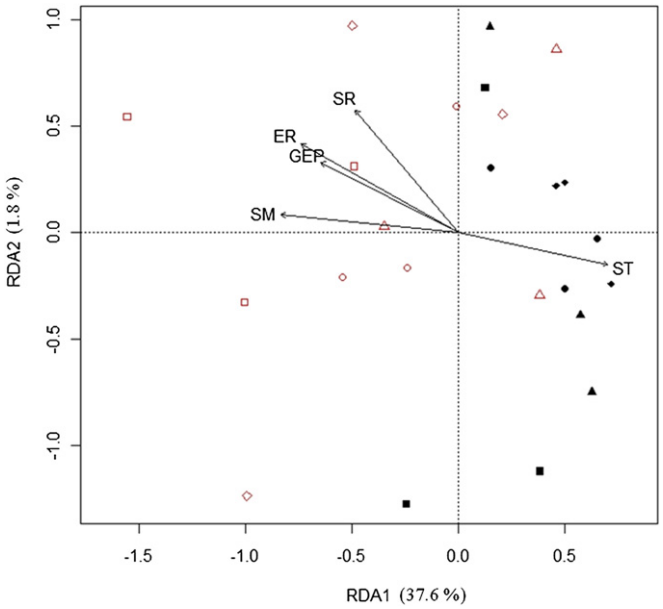

Fig. 5. Associations of microbial C utilization patterns with soil microclimate and ecosystem C exchange. Constrained axes RDA1 and RDA2 can account for 37.6% and 1.8% of total variations, respectively. Solid squares, solid circles, solid triangles and solid diamonds represent the control, day warming, night warming, and diurnal warming in 2006, respectively. Hollow squares, hollow circles, hollow triangles and hollow diamonds represent the control, day warming, night warming, and diurnal warming in 2007 respectively. SM, soil moisture; ST, soil temperature; GEP, gross ecosystem productivity; ER, ecosystem respiration; SR, soil respiration.

et al. 2009; Xia et al., 2009) indicate the key roles of plant physiology in triggering microbial activities. Our results provide indirect evidence in support of Högberg and Reads' (2006) assumption that physiological continuity and dynamic interdependence exist in plant–microbe–soil system.

At global scale, asymmetrically diurnal warming with greater increase in daily minimum than maximum temperature has been widely observed (Karl et al., 1991; Easterling et al., 1997, 2000; Rebetez, 2001; IPCC, 2001; Alexander et al., 2006). There are significant increases in annual occurrence of warm nights over about 75% of sampled global land areas, especially in Eurasia (Liu et al., 2004; Alexander et al., 2006). Since night warming can trigger much stronger responses of some specific microbial groups with their C utilization potential and ecosystem C exchange, soil microbes in those regions with asymmetrically diurnal warming may be more sensitive than those in other areas, and their responsive activities will, to some extent, modify ecosystem C exchange.

5. Conclusion

There were significant interannual differences in microbial community composition and C use patterns during the 2-year experimental period. The findings that day and night warming differently influenced some specific microbial groups and microbial C utilization potential are in line with our hypothesis. Variations in the relative proportion of specific microbial groups and microbial C utilization potential under asymmetrically diurnal warming suggest tight linkages of microbial groups to their physiological traits. Altered hydro-thermal constraints could partially account for the microbial compositional and physiological changes. The potential competition for amino compounds between plants and soil microbes could explain night warming-caused reductions in microbial C utilization potential, especially the use potentials of amino compounds. Close correlations between microbial C utilization patterns and ecosystem C exchange suggest that coupled physiological responses of plants and microbes exist. These findings highlight physiological continuity and dynamic interdependence of microbial-mediated plant-soil system.

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