Reference for different sensitivities of greenhouse gases effluxes to warming climate among types of desert biological soil crust

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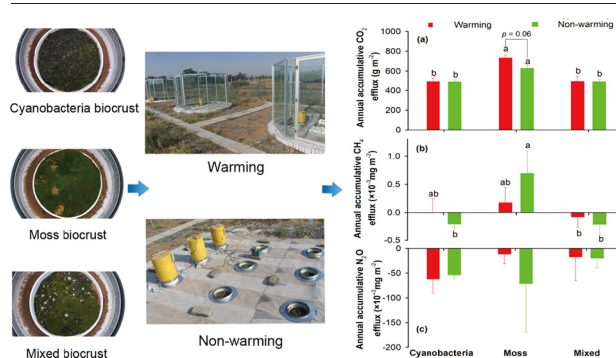[c] Eastern Oregon Agriculture and Natural Resource Program, Oregon State University, La Grande, OR, USA

HIGHLIGHTS

- Respiratory C release in moss-dominated biocrust was higher than in cyanobacteria-dominated and mixed biocrusts.
- The desert biocrust soils mostly acted as a weak sink of atmospheric CH_4 and N_2O.
- Warming decreased ($p = 0.06$) annual accumulative CO_2 efflux for moss-dominated biocrust.
- Warming caused a kind of suppression of CH_4 and N_2O emissions for moss-dominated biocrust.

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

There is much uncertainty about how climate warming will impact greenhouse gases (GHG) budget in dry environments due to the lack of available data for desert biocrust soil. We implemented a 2.5-year field measurement of CO_2, CH_4 and N_2O effluxes in cyanobacteria-dominated, moss-dominated and mixed (cyanobacteria, moss and lichen) biocrust soils using open-top-chambers to simulate climate warming (1.2 °C on average). Desert biocrust soils generally acted as a weak sink of atmospheric CH_4 and N_2O. Although warming effects on daily CO_2, CH_4, and N_2O effluxes varied depending on sampling date and biocrust soil, there was no significant difference in daily, monthly and seasonal average CO_2, CH_4 and N_2O effluxes between warming and control in most cases for three biocrust soils. However, warming caused a marginal ($p = 0.06$) decrease (14.2%) in annual accumulative CO_2 efflux in moss-dominated biocrust soil due to the drought effects caused by warming indirectly and OTC sheltering of precipitation directly, while there was no significant difference between warming and control for cyanobacteria-dominated and mixed biocrust soils, implying a neutral response of GHG effluxes to climate warming. These results suggest that the GHG budget in arid desert biocrust soil would not be significantly changed in the warmer future when the direct negative effects of drought on CO_2 effluxes were excluded. Therefore, a marginal decrease of accumulative CO_2 effluxes in response to warming coupled with drought for moss-dominated biocrust soil might offer a weak negative feedback to warming and drier climate change pattern.

1. Introduction

Terrestrial ecosystems act as important sources or sinks of atmospheric greenhouse gases (GHGs) (Dijkstra et al., 2013; Wang et al., 2014). Global surface temperature in the 21st century has increased by 1.59 °C compared to the last half of the century (IPCC, 2021). The semiarid and arid regions

are predicted to experience a two-fold increase in surface temperature as compared to the humid regions (Huang et al., 2016) combined with drier condition (Dai, 2013; Trenberth et al., 2014). Even small variations in GHGs (CO_2, CH_4 and N_2O) effluxes in response to climatic change can give rise to important feedbacks to climate change, which has attracted intense attention across various ecosystems (Dijkstra et al., 2013; Hu et al., 2010; Lafuente et al., 2020; Marotta et al., 2014; Voigt et al., 2016; Ward et al., 2013). However, previous studies mainly focused on GHGs budgets from farmland, forest, grassland and peatland (Reynolds et al., 2007; Tian et al., 2020; Wang et al., 2014), whereas comparably few studies contribute to similar understanding relative to desert ecosystems (e.g. Guan et al., 2021; Lafuente et al., 2020). While desert being characterized by sparse plant cover and poor nutrients availability mainly controlled by rainfall events (Whitford and Wade, 2002), changes in soil C and N in the form of gaseous C (CO_2 and CH_4) and N (e.g. NO_x) release due to climate warming might have an important impact on atmospheric GHGs budgets given that 41% of the global terrestrial surface is considered arid environment (Castillo-Monroy et al., 2011). However, there are still large uncertainties associated with estimates of GHG budgets in deserts due to a lack of available data, especially during the winter.

Biological soil crust (biocrust hereafter), an association of soil particles with cyanobacteria, mosses, lichens, bacteria, fungi and archaea in different proportions, are widely distributed in drylands as the dominant surface landscape (Belnap et al., 2016; Weber et al., 2015). Besides functions of improving soil fertilization and stability, sand fixation, soil erosion prevention, etc., biocrusts also play vital roles in C (Elbert et al., 2012; Grote et al., 2010; Li et al., 2012) and N (Abed et al., 2013; Belnap, 2002; Elbert et al., 2012; Weber et al., 2015) cycling. It is estimated that biocrust microsites contribute 42–66% of the total respiratory C release in arid and semiarid ecosystems (Castillo-Monroy et al., 2011; Morillas et al., 2017; Zhao et al., 2016). Furthermore, a previous incubation study revealed that biocrust soil can release CH_4 through anaerobic methanogenesis in anoxic condition (Angel et al., 2011). In addition, there is a high potential of N_2O emission in arid wet biocrust soil via denitrification and nitrification (Abed et al., 2013; Crenshaw et al., 2008). Thus, it seems that a considerable CH_4 and N_2O emission after rainfall events might be an important source of atmospheric CH_4 and N_2O (Abed et al., 2013; Angel et al., 2011; Zaady et al., 2013). However, field measurements of CO_2, CH_4 and N_2O effluxes in different arid biocrust soils in response to climate warming are still scarce to date.

Many biological processes in desert soil have been reported to depend on soil moisture (Grote et al., 2010; Morillas et al., 2017). What previous studies focus on is the response of GHGs effluxes to climate change and specifically water-change effects on respiration (Sponseller, 2007; Talmon et al., 2011; Zhao et al., 2016). However, many studies have found that dryland soil gaseous C and N effluxes are also highly sensitive to temperature changes (Abed et al., 2013; Dijkstra et al., 2013; Lafuente et al., 2020; Morillas et al., 2017). For instance, even a 0.34 °C of warming can cause a larger change in respiration sensitivity in desert soil than other biomes (Carey et al., 2016). Dijkstra et al. (2013) found that warming can reduce the net sink of CH_4 and N_2O in a semiarid grassland due to decreased soil moisture. A recent study found that the responses of CH_4 and N_2O effluxes in semi-arid biocrust soil to warming depended on biocrust cover (Lafuente et al., 2020). Thus, climate warming might affect GHGs effluxes budgets in desert biocrust soil and give rise to an important feedback to climatic change regulated by soil water condition. Desert biocrust ecosystems are highly variable in their compositions due to topographic difference and these biocrusts undergo various stages of succession from cyanobacteria-dominated early stages to cyanobacteria-moss-lichen mixed later stages (Li, 2012; Tucker et al., 2019) in their development. Thus, it is highly necessary to investigate how desert biocrust soils with different cryptogams in composition respond to climate warming with the objective to accurately predict GHG budgets in drylands in the future.

Here, a field warming experiment with open-top-chambers (OTCs) was established to examine warming effects and its combination of drought on GHGs effluxes. The CO_2, CH_4 and N_2O effluxes in cyanobacteria-, moss-, and mixed (moss, cyanobacteria and lichen) biocrust soils were measured from 2012 to 2014, covering three growing seasons and two non-growing seasons. The objectives were to: (i) reveal CO_2, CH_4 and N_2O effluxes and the variation pattern of different biocrust soils; (ii) examine warming effects on CO_2, CH_4 and N_2O effluxes of different biocrust soils at various temporal scales (daily, monthly, seasonally and annually), and (iii) estimate annual GHGs budgets of different biocrust soils.

2. Material and methods

2.1. Site description

We conducted this study in the field OTC warming experiment at the Shapotou Desert Research and Experimental Station (SDRES) (37°33′N, 105°02′E, elevation = 1250 m a.s.l.) of the Chinese Academy of Sciences, located at the southeast edge of the Tengger Desert, China. The climate is a typical continental arid climate with an average annual temperature of 10.0 °C and annual rainfall of 182.6 mm in the past 50 years (1955–2016). More than 90% of precipitation falls during summer and autumn from July to September. This region is characterized as a transitional zone from desert to steppe. The main soil is classified as Orthic Sierozeme and aeolian sandy soil according to FAO classification system. Our sampling site is a natural desert ecosystem situated in the west of SDRES, about 30 km away,. Vegetation is a mixture of drought-tolerant shrubs and grasses dominated by *Artemisia ordosica* Krasch., *Caragana korshinskii* Kom., *Artemisia capillaris* Thunb. and *Eragrostis minor* Host., with an average canopy coverage of about 35%. Soil biocrusts distributed in the open surface soil among shrub patches differ in composition of cyanobacteria, moss and lichen with more than 80% coverage. The dominant cyanobacteria and lichen species include *Microcoleus vaginatus and Phormidium tenue* (Hu et al., 1999), *Candelariella antennaria* (Liu and Wei, 2013). The moss biocrusts are dominated by *Bryum argenteum, Didymodon constrictus, Tortula bidentata*, etc. (Li et al., 2003).

2.2. Experiment design

In June 2012, cyanobacteria-dominated (>80% sample plot cover), moss-dominated (>85% sample plot cover), and mixed biocrust soils (about 50, 40 and 8% sample plot cover of moss, cyanobacteria and lichen) were randomly selected in a 400 m² square area. Six intact soil columns (diameter × depth = 0.2 × 0.25-m) of each biocrust soil were randomly collected using PVC tubes. The biocrust surface was water-wetted before collection to avoid fragmentation during the sampling process. These collected intact soil columns were then taken back to SDRES. Three intact soil columns for each biocrust soil were averagely placed in three OTCs as warming (W), and the other three soil columns were placed outside of the OTCs as control (NW). All soil columns were leveled to the ground, and the surrounding soil surface was covered by plastic gauze to prevent burial due to sand events.

The OTCs, regular octagons with 1.3-m in length and 2-m in height of glass side, were established in 2009. Two sets of HOBO U30 weather stations (Onset Computer Corporation, Bourne, MA, USA) were installed in the center and outside of the OTC to monitor soil moisture at 10-cm depth, whereas soil moisture within 5 cm-depth topsoil could not be well continually recorded due to the very dry soil condition and susceptibility to sand burial and wind erosion. Data was automatically recorded and stored every 30 min. Soil temperature at 5-cm depth was measured using digital thermometers (JM624, Jinming Corporation, China) when gas samples were collected.

2.3. Measurements of CO_2, CH_4 and N_2O effluxes

We measured CO_2, CH_4 and N_2O effluxes using static chamber and gas chromatography techniques about every 10 days during the growing season (May to October) depending on weather conditions and once a month during the non-growing season (November to April). The structure of static

chambers is similar to that in Hu et al., 2010, which consisted of a bottom anchor (0.25-m diameter × 0.2-m height) with a top 3-cm depth circle groove connected to a PVC column (0.25-m diameter) that was inserted into the soil about 15-cm below the soil surface, and a removable cover cylinder (0.25-m diameter × 0.4-m height) with a fan attached to the inside top wall and an outside white cloth to prevent sunlight warming. The cover cylinder was placed on the bottom anchor and sealed with water during the sampling period. Static chambers were closed for 30 min and 4 gas samples (about 25 ml) were manually collected from the closed chambers every 10 min using 50 ml plastic syringes between 9:00 and 11:00 a.m. The concentration of CO_2, CH_4 and N_2O in gas samples was analyzed using gas chromatography (Agilent 6820, Palo Alto，USA) within 12 h after sampling. The effluxes were calculated as the slope of linear regressions from the measured gas concentrations with time (Morillas et al., 2017).

2.4. Statistical analysis

Normality was tested for CO_2, CH_4 and N_2O effluxes (SPSS Inc. version 25.0, Chicago, USA). Nonparametric test with Mann-Whitney U test was used to test significant difference of daily, monthly and seasonally CO_2, CH_4 and N_2O effluxes between warming and control for each biocrust soil at the $p < 0.05$ level. Nonparametric test with Jonckheere-Terlstra test was used to test significant difference in annually average CO_2, CH_4 and N_2O effluxes that did not meet normality among different biocrust soils, and one way ANOVA and Least Significance Difference (LSD) were used to test significant difference in annually average CO_2, CH_4 and N_2O effluxes that meet normality and accumulative CO_2, CH_4 and N_2O effluxes among different biocrust soils. Linear regression and exponential functions were

performed to test the dependency of CO_2, CH_4 and N_2O effluxes on soil temperature and moisture. The detailed calculation of Q_{10} value for respiratory C release referred to that in Dacal et al. (2020).

3. Results

3.1. Soil temperature and moisture

Compared to the control (non-warming), warming increased soil temperature by 1.2 °C and decreased soil moisture by 39.7% on average from July 2012 to December 2014 (Fig. 1). Warming increased average annual soil temperature by 1.6, 0.8 and 1.0 °C, and decreased average annual soil moisture by 34.5, 41.5 and 39.4% in 2012 (since July), 2013 and 2014, respectively. Warming increased soil temperature by 0.9 and 1.3 °C during the growing season and non-growing season, and decreased soil moisture by 37.8 and 56.4% during the growing season and non-growing season, respectively. These results indicate that the OTCs created warmer and drier climatic conditions, especially during the non-growing season.

3.2. CO_2 efflux

In general, warming effects on daily CO_2 efflux varied depending on sampling date and biocrust soils. Daily CO_2 efflux showed a unimodal variation pattern with minimum values in January–February and peaks in June–July across three biocrust soils (Fig. 2). In terms of non-warming (control), the average CO_2 efflux of moss-dominated biocrust soil (97.8 ± 13.8 mg m^{-2} h^{-1}) was significantly higher than that of cyanobacteria-dominated (67.3 ± 8.6 mg m^{-2} h^{-1}) and mixed biocrust soil (65.9 ±
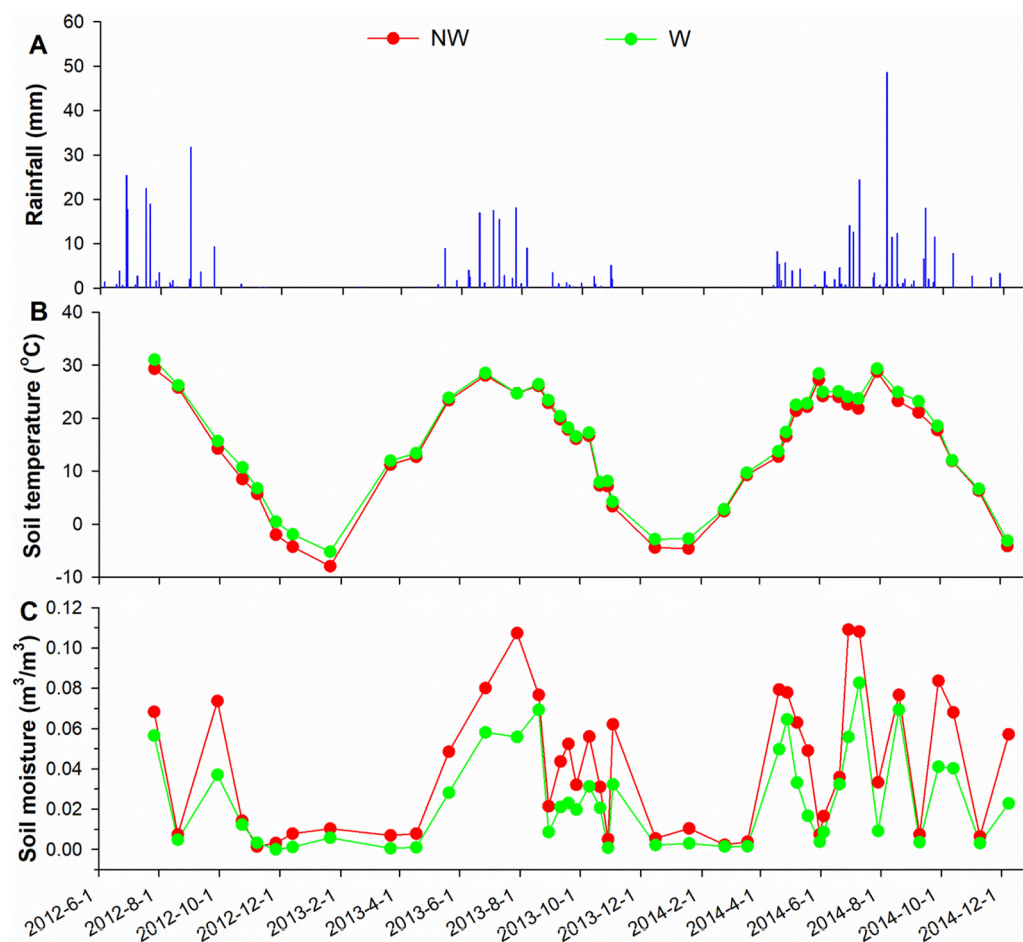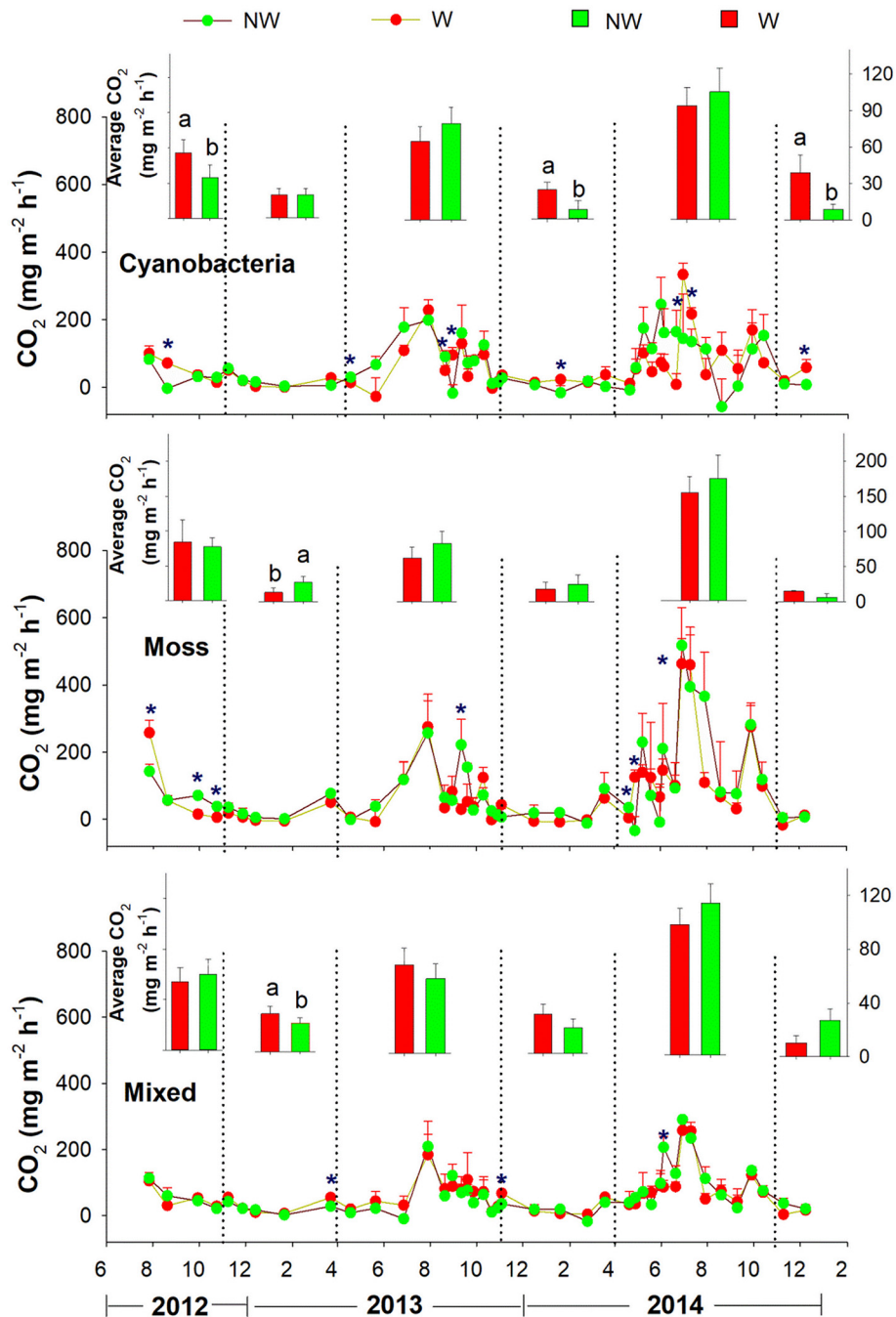

Fig. 1. The amount of rainfall (A), soil temperature at 5-cm depth (B) and soil moisture at 10-cm depth (C) under warming (W) and control (NM) over 2012–2014.

Fig. 2. The monthly and seasonal average CO_2 effluxes for different biocrust soils under warming (W) and non-warming (NW). Bars are standard error. Asterisks and different lowercase letters denote significant differences in daily and average seasonal CO_2 effluxes between W and NW at $p = 0.05$ level, respectively.

6.8 mg m^{-2} h^{-1}) over 2012–2014. The average CO_2 efflux for cyanobacteria (96.4 ± 10.7 mg m^{-2} h^{-1}), moss (132.0 ± 23.4 mg m^{-2} h^{-1}) and mixed biocrust soil (85.0 ± 13.2 mg m^{-2} h^{-1}) during the growing season were 6.8-, 5.0- and 4.0-fold higher than that during the non-growing season, respectively. Annual average CO_2 efflux for moss-dominated and mixed biocrust soils in 2013 was significantly ($p < 0.05$) lower than that in 2014, while there was no significant difference for cyanobacteria-dominated biocrust soil between the two years (Fig. 5A).

Despite no significant difference in daily CO_2 efflux between warming and control was found for three biocrust soils over 2012–2014 in most cases (Fig. 2), warming decreased the average CO_2 efflux by 4.4, 15.0 and 2.4% for cyanobacteria-dominated, moss-dominated and mixed biocrust soil over 2012–2014, respectively, indicating that moss-dominated biocrust soil might be more sensitive to climatic warming and its combination of

drought than the other two biocrust soils. At the monthly scale, warming significantly decreased the average CO_2 efflux in May (by 67.8%) and October (by 40.8%) for cyanobacteria-dominated biocrust soil, and significantly increased the average CO_2 efflux in March (by 60.3%) for mixed biocrust soil (Fig. 5A). Warming significantly increased the average CO_2 efflux by 58.9, 28.4, 35.1 and 32.3% for cyanobacteria-dominated soil during the growing season in 2012 and non-growing season in 2013–2014 and 2014, and mixed biocrust soil during the non-growing season over 2012–2013, respectively. However, warming significantly decreased the average CO_2 efflux by 50.8% for moss-dominated biocrust soil during the non-growing season over 2012–2013, whereas there was no significant effects on average seasonal (growing season and non-growing seasons) and annual CO_2 efflux between warming and control in other periods (Figs. 2 and 5A).

3.3. CH₄ efflux

CH₄ uptake (as indicated by negative efflux) and emission (as indicated by positive efflux) events were detected across three biocrust soils, and most emission events mainly occurred during the growing season (Fig. 3). The average daily CH₄ efflux varied with the range from -1.1 (cyanobacteria-dominated biocrust under non-warming) to 1.4 μg m^{-2} h^{-1} (cyanobacteria-dominated biocrust under non-warming) for three biocrust soils over 2012–2014, showing no evident variation pattern over the year. The cyanobacteria-dominated and mixed biocrust soils mostly showed CH₄ uptakes, while moss-dominated biocrust soil showed CH₄ releases in most months (Fig. 5B) largely due to more CH₄ emissions in 2014 (Fig. 3). As for non-warming (control), moss-dominated biocrust soil (0.002 μg m^{-2} h^{-1}) during the non-growing season showed a

significantly ($p = 0.02$) higher CH₄ efflux than the other two biocrust soils. The average CH₄ efflux for cyanobacteria-dominated biocrust soil in 2014 was significantly higher than that in 2013 (Fig. 5B). However, there was no significant difference in the average CH₄ efflux among different biocrust soils over 2012–2014.

Warming had no significant effects on daily, monthly, seasonal and annual average CH₄ efflux for three biocrust soils in most cases (Figs. 3 and 5B). However, warming caused a significant increase (by 150.0%) of CH₄ uptake for cyanobacteria-dominated biocrust soil during the growing season in 2014 and a decrease (by 33.3%) of CH₄ uptake for mixed biocrust soil during the non-growing season over 2013–2014 (Fig. 3). Warming also significantly increased (by 585.9%) average annual CH₄ uptake for cyanobacteria-dominated biocrust soil in 2014 compared to the control (Fig. 5B).
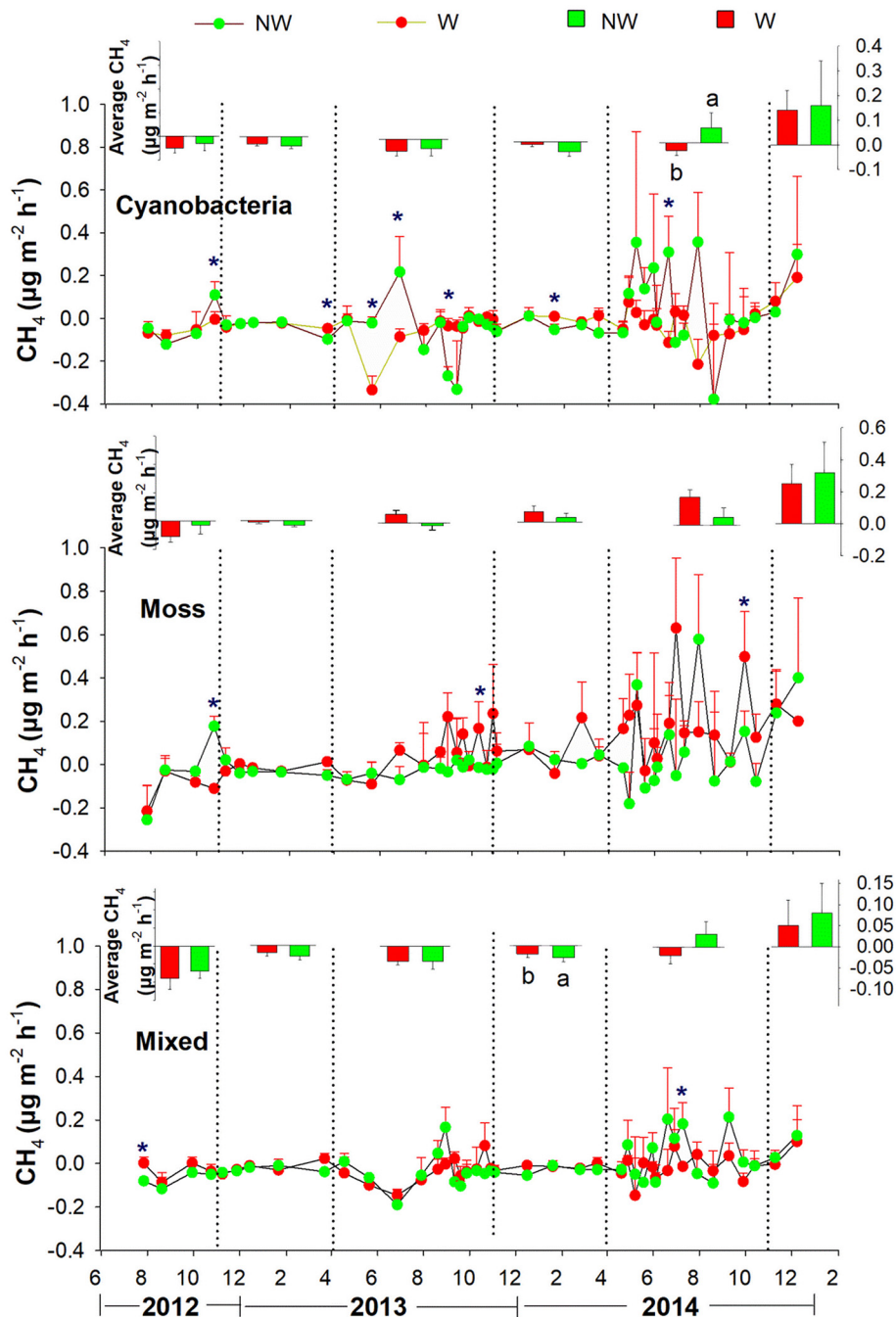

Fig. 3. The monthly and seasonal average CH₄ effluxes for different biocrust soils under warming (W) and non-warming (NW). Bars are standard error. Asterisks and different lowercase letters denote significant differences in daily and average seasonal N₂O effluxes between W and NW at $p = 0.05$ level, respectively.

3.4. N₂O efflux

N₂O emission (as indicated by positive efflux) and uptake (as indicated by negative efflux) events were observed during both growing season and non-growing season for three biocrust types with the range from −181.3 (moss-dominated biocrust soil under warming) to 205.0 μg m⁻² h⁻¹ (mixed biocrust soil under warming), which showed a fluctuation pattern over the year (Fig. 4). Based on the monthly scale, three biocrust soils showed N₂O uptake in most months (Fig. 5). In the cases of non-warming (control), no significant difference in seasonal (growing season and non-growing season) and annual average N₂O efflux was found among different

biocrust soils across 2012–2014. However, the average N₂O efflux for cyanobacteria-dominated biocrust soil in 2014 was significantly lower than that in 2013 (Fig. 5C).

In general, there was no significant difference in daily, monthly, seasonal and annual average N₂O efflux between warming and control for three biocrust soils (Figs. 4 and 5C). However, warming significantly increased the average N₂O uptake of cyanobacteria-dominated biocrust soil in September, and altered N₂O efflux of moss-dominated biocrust soil from net uptake/emission to net emission/uptake in April and November, respectively (Fig. 5C). Warming only significantly increased the average N₂O uptake of cyanobacteria-dominated biocrust soil in 2012 (Fig. 5C).
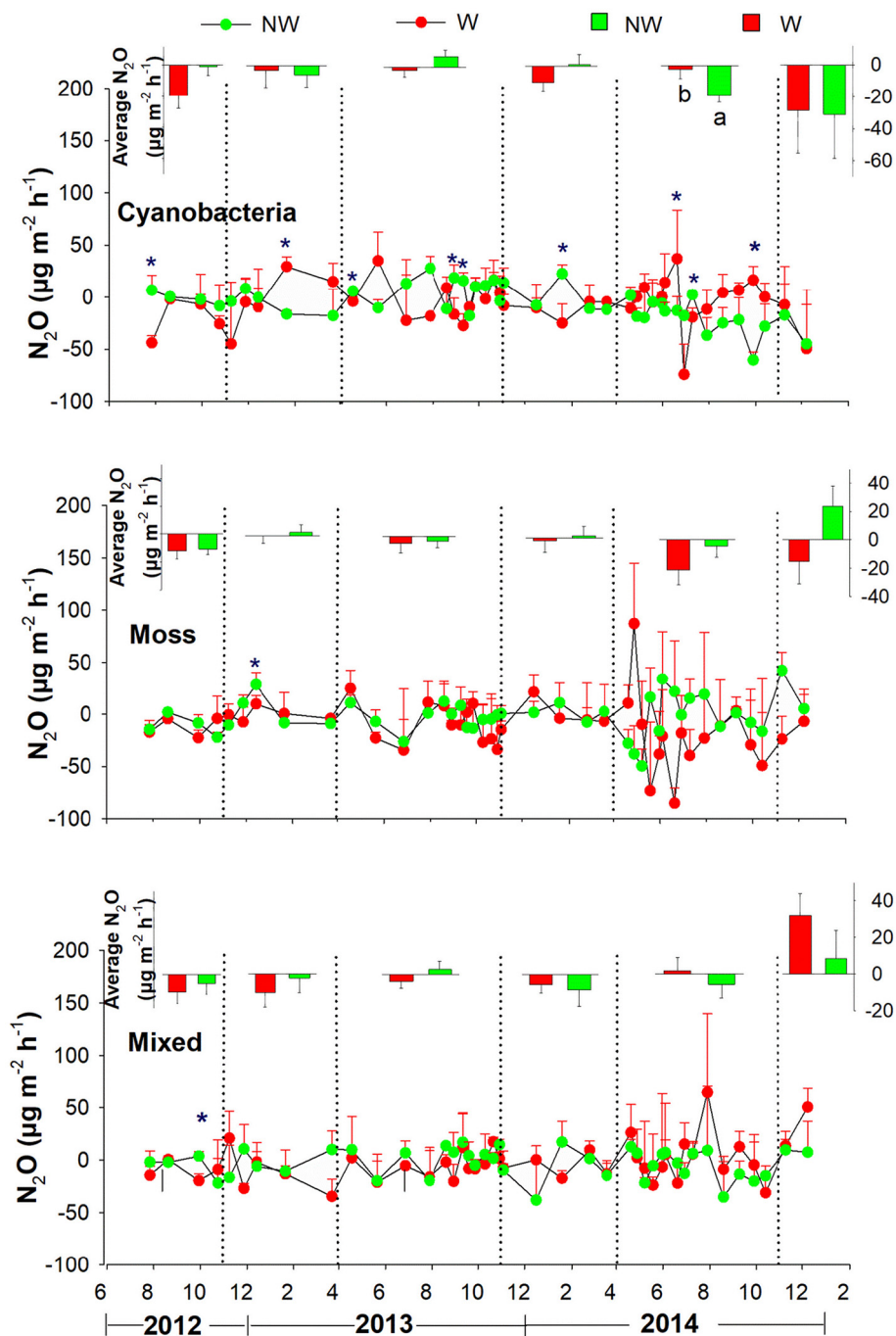

Fig. 4. The monthly and seasonal average N₂O effluxes for different biocrust soils under warming (W) and non-warming (NW). Bars are standard error. Asterisks and different lowercase letters denote significant differences in daily and seasonal average N₂O effluxes between W and NW at $p = 0.05$ level, respectively.
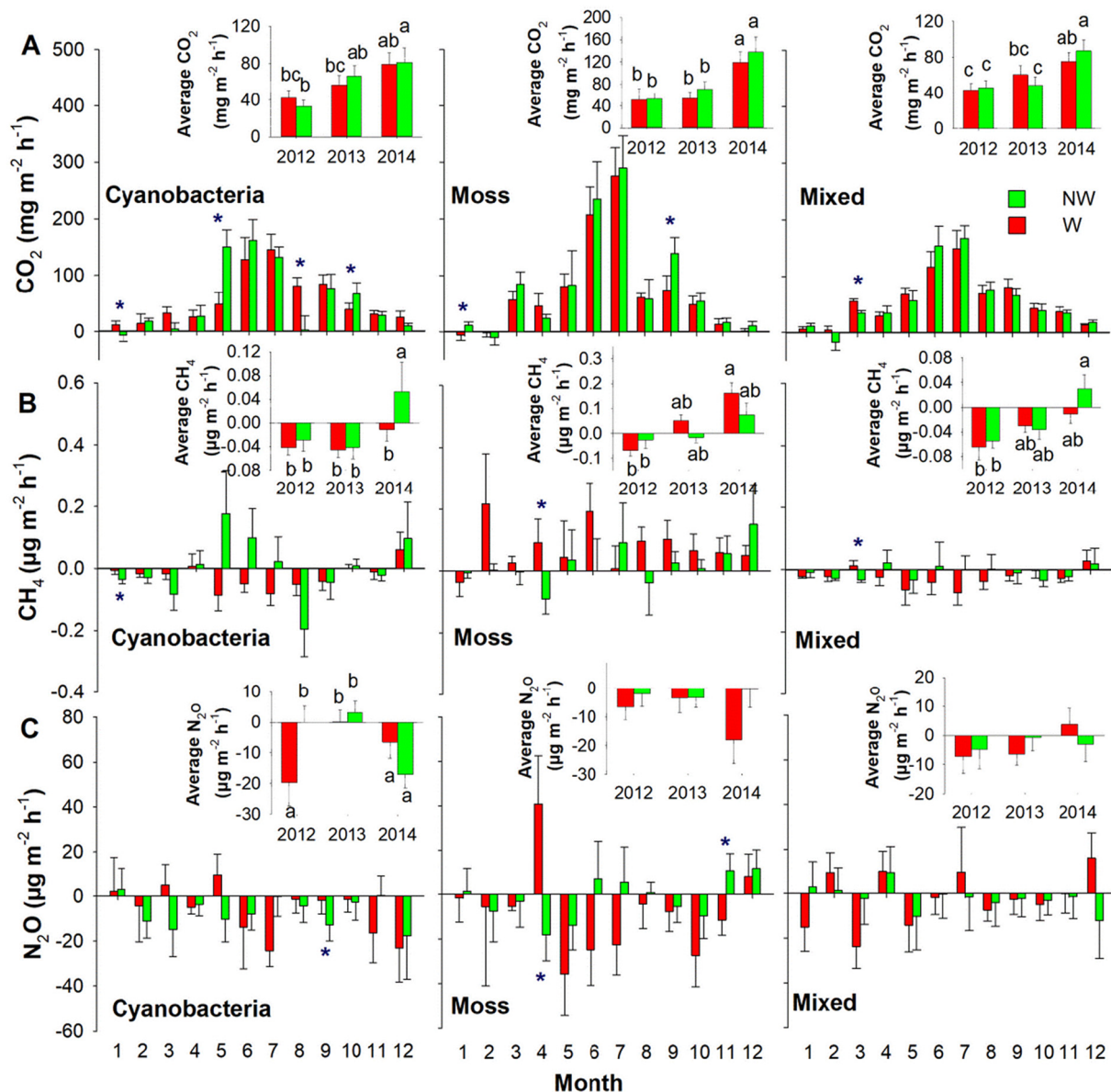
Fig. 5. Comparison of warming effects on monthly and annual average CO_2 (A), CH_4 (B) and N_2O (C) effluxes for different biocrust soils. Bars are standard error. Asterisks and different lowercase letters denote significant differences in monthly and annual average CO_2, CH_4 and N_2O effluxes at $p = 0.05$ level, respectively.

3.5. Accumulative budgets of CO_2, CH_4 and N_2O effluxes

The annual accumulative CO_2 efflux for three biocrust soils ranged from 494.2 (mixed biocrust soil under warming) to 732.7 g m^{-2} (moss-dominated biocrust soil under non-warming). The accumulative CH_4 efflux for moss-dominated biocrust soil under non-warming was significantly higher than that for mixed biocrust soil under non-warming. Warming decreased (by 14.2%) annual accumulative CO_2 release for moss-dominated biocrust soil at the marginal significant level ($p = 0.06$). There was no significant difference in annual accumulative CH_4 and N_2O effluxes between warming and control for three biocrust soils (Table 1).

3.6. Relationships of CO_2, CH_4 and N_2O effluxes with abiotic factors

CO_2 efflux was positively exponentially related to soil temperature for three biocrust soils under warming and non-warming, soil temperature explained 20.0% (cyanobacteria-dominated biocrust soil under warming) to 44.1% (moss-dominated biocrust soil under non-warming) of variation in

daily CO_2 efflux. Warming decreased temperature sensitivity (Q_{10}) of CO_2 efflux for cyanobacteria-dominated biocrust soil and increased that for moss-dominated biocrust soil, while Q_{10} for mixed biocrust soil under warming and non-warming was almost the same. Daily CO_2 efflux linearly

Table 1
Annual accumulative CO_2, CH_4 and N_2O effluxes for different biocrust soils under warming (W) and non-warming (NW). Average and standard error in parentheses were shown. Different lowercase letters represent significant difference among different biocrust soils.

Biocrust	Treatment	CO_2 (g m^{-2})	CH_4 ($\times 10^{-3}$ mg m^{-2})	N_2O ($\times 10^{-3}$ mg m^{-2})
Cyanobacteria	NW	494.8(34.7)[b]	0.0(0.2)[ab]	−61.9(27.9)
	W	492.9(18.8)[b]	−0.2(0.1)[b]	−53.7(7.7)
Moss	NW	732.7(30.7)[a]	1.8(2.7)[a]	−11.7(19.2)
	W	628.9(27.3)[a]	0.7(0.4)[ab]	−71.3(98.2)
Mixed	NW	496.0(48.1)[b]	−0.1(0.2)[b]	−17.5(47.8)
	W	494.2(23.3)[b]	−0.2(0.2)[b]	−20.0(18.9)

increased with an increase in soil moisture, which explained 13.8% (cyanobacteria-dominated biocrust soil under non-warming) to 32.0% (mixed biocrust soil under warming) of variations in daily CO_2 efflux across three biocrust soils (Table 2). CH_4 efflux for cyanobacteria-dominated ($p < 0.001$) and mixed biocrust soils ($p = 0.012$) under warming were negatively linearly correlated with soil temperature with an explanation of 5.0–8.2% for daily CH_4 effluxes variation. N_2O efflux was not associated with soil temperature for three biocrust soils under warming and non-warming. Both CH_4 and N_2O effluxes were not in relation to soil moisture for three biocrust soils under warming and non-warming.

4. Discussion

4.1. Respiratory C release

Cryptogam composition generally successes from cyanobacteria dominance in the early stage to lichen-moss mixed dominance in the later stage in drylands (Li et al., 2012; Tucker et al., 2019). Meanwhile, soil nutrients level, cryptogam and microbial biomasses often improved during the succession process (Hu et al., 2019; Zhao et al., 2016). Similar to previous studies (Zhao et al., 2016), our results showed higher respiration in moss-dominated biocrust soil than cyanobacteria-dominated and mixed biocrust soil under non-warming (Figs. 2 and 5A, Table 1). The relatively higher CO_2 efflux for moss-dominated biocrust soils probably resulted from both autotrophic respiration due to higher biomass of cryptogams (Li et al., 2018) and heterotrophic respiration owing to higher soil microbial biomass and nutrients level (Hu et al., 2020; Zhao et al., 2016). Furthermore, higher abundance of the C-cycling related gene in the later succession stage could be responsible for higher respiration due to the higher C-respiration potential (Hu et al., 2019). The amount of respiratory C release (135.3–199.8 g m^{-2} y^{-1}) was higher than the estimates based on field measurements during the growing season in a 56-year artificial revegetation region (67.9–128.8 g m^{-2} y^{-1}) and modeling estimates (101.0–135.5 g m^{-2} y^{-1}) in a semiarid biocrust soil (Castillo-Monroy et al., 2011). The respiration of the biocrust soils under non-warming during the non-growing season accounted for 7.8–12.1% of the annual accumulative CO_2 efflux, suggesting that respiratory C release during the winter should be taken into consideration when we estimate respiratory C release in arid desert ecosystems.

In water-limited desert ecosystems, respiratory C release strongly relies on the amount of rainfall (Talmon et al., 2011; Zhao et al., 2016). An enhanced soil water availability may trigger microbial respiration even after light rain events (Garcia-Palacios et al., 2018; Thomas et al., 2011), evidenced by the positive relationship between CO_2 efflux and soil moisture in our study (Table 2). By contrast, biological activities of soil microorganisms and enzymes would be inhibited in the drought conditions (Garcia-

Palacios et al., 2018; Hu et al., 2020; Talmon et al., 2011). Meanwhile, biocrusts are an assembly of poikilohydric organisms that can be metabolically inactive when there is no water available and quickly return to active status after rehydration (Belnap et al., 2016; Darrouzet-Nardi et al., 2015). Thus, more than 95% of annual precipitation coupled with higher temperature during the growing season in this region contributed much higher CO_2 efflux than that during the non-growing season. We also observed impulses of CO_2 efflux after rain events (Fig. 2) originated from improved liable C from photosynthetic products and autotrophic respiration due to metabolically active function of cryptogams (Belnap et al., 2016). Thus, the higher CO_2 efflux in 2014 than that in 2013 could be ascribed to its much higher annual precipitation (263.9 mm in 2014 vs. 127.0 mm in 2013). More effective rainfall events (11 events in 2014 and 6 events with more than 5 mm in 2013, 7 and 3 events with more than 10 mm in 2014 and 2013, respectively) might be responsible for higher variability of respiration C release. These findings highlight the importance of soil water availability in determining respiratory C release from arid biocrust desert soil. The drier the local conditions, the greater effects of water availability on respiration (Talmon et al., 2011).

Despite several significant changes in daily, monthly and seasonal average CO_2 efflux were detected, warming mostly did not change CO_2 efflux for three biocrust soils (Figs. 2 and 5A). This could be partially ascribed to limited effects of warming on organic matter and nutrients availability (Zelikova et al., 2012). However, warming decreased accumulative annual CO_2 effluxes for moss-dominated biocrust soil, while there was no difference between warming and control for cyanobacteria-dominated and mixed biocrust soils. These findings indicate that the respiratory C release from moss-dominated biocrust soil might be more sensitive to climate warming than the other two biocrust soils. Previous studies have found different responses of respiration to warming in desert biocrust soils, with reported positive (Dacal et al., 2020; Darrouzet-Nardi et al., 2015), neutral (Dacal et al., 2020) and negative (Carey et al., 2016; Garcia-Palacios et al., 2018) effects depending on the amount of local precipitation and the extent of warming-caused soil drying. These results reflected that effects of increased temperature on respiration in drylands could be regulated by soil water availability largely determined by rainfall. Less respiratory C release in warming conditions could be attributed to both reduction of moss-dominated biocrust biomass (Li et al., 2018) and moisture limitation due to warming-induced reduction of water availability (Tucker et al., 2019) and inhibition of enzyme activities (Hu et al., 2020). Thus, the response of respiratory C release to warming was closely linked to the offsets between direct warming effects and indirect drought effects caused by warming. Probably, warming might inhabit microbial respiration and autotrophic respiration of cryptogams due to reduction in moss-dominated biocrust biomass (Li et al., 2018) and shortening of wet soil duration (Garcia-Palacios et al., 2018). Moreover, the reduction in precipitation due to OTC sheltering could not be ignored that might further strengthen the inhabitation for respiratory C release. Therefore, the discrepancy between our findings and previous studies might be a consequence of the amount of local rainfall and warming-induced soil moisture reduction extent (Dacal et al., 2020). For instance, warming caused an increased respiration coupled by a 1.5% of reduction in soil moisture in a Mediterranean semiarid biocrust soil with 336 mm precipitation (Dacal et al., 2020). The response of our measurements to warming was regulated by more than 35% decrease in soil moisture with an average precipitation of 188.2 mm during the past 54 years from 1956 to 2009. Additionally, biocrust respiration was also associated with dew generation and inputs that were enough to drive desert biocrust respiration (Delgado-Baquerizo et al., 2013). Although we have no available data about dew formation and duration, a shorter dew-wet duration could be expected due to warming-caused enhanced evaporation. Given suppression of respiration due to reduced soil moisture caused by warming, OTC sheltering of precipitation and shortened dew duration, warming did not change annual average CO_2 efflux for three biocrust soils in most cases (Figs. 2 and 5). However, we were

Table 2

Exponential ($Y = ae^{bT}$) and linear relationships ($Y = aX + b$) between CO_2 efflux (Y) and soil temperature (T) and soil moisture (X), and temperature sensitivity (Q_{10}) for different biocrust soils under warming (W) and non-warming (W).

Biocrust	Treatment	a	b	p	R^2	Q_{10}
$Y = ae^{bT}$						
Cyanobacteria	NW	13.00	0.076	<0.001	0.349	2.16
	W	14.87	0.064	<0.001	0.200	1.90
Moss	NW	18.66	0.088	<0.001	0.441	2.41
	W	9.01	0.107	<0.001	0.378	2.91
Mixed	NW	17.38	0.062	<0.001	0.437	1.86
	W	16.25	0.061	<0.001	0.374	1.83
$Y = aX + b$						
Cyanobacteria	NW	1022.37	43.18	<0.001	0.138	–
	W	1582.84	33.27	<0.001	0.255	–
Moss	NW	2053.13	38.14	<0.001	0.207	–
	W	2867.30	23.97	<0.001	0.304	–
Mixed	NW	1130.44	30.39	<0.001	0.269	–
	W	1677.70	30.31	<0.001	0.320	–

unable to distinguish the separate effects of warming from drought suppression. Therefore, we speculate that respiratory C release in the arid desert biocrust soil might not be significantly changed in the warmer future when the negative effects of OTC-sheltering of precipitation were excluded.

4.2. CH$_4$ uptake

Generally, CH$_4$ is produced by methanogenesis under anaerobic condition and oxidized by methanotrophs under aerobic conditions (Lafuente et al., 2020). The biocrust soils mostly acted as a sink of atmospheric CH$_4$ (Fig. 3), indirectly confirmed by considerable abundance of CH$_4$-oxidation related gene (*pmoA*) in biocrust soils (Hu et al., 2019; Lafuente et al., 2020). Lafuente et al. (2020) observed higher CH$_4$ uptake in the biocrust soil with high (vs. low) cover due to higher abundance of *pmoA* in the Mediterranean semi-arid ecosystem. However, our result showed that seasonal and annual average CH$_4$ effluxes in different biocrust soils were not significantly differed from each other in most cases. This might be a consequence, at least partially, of the comparable abundance of *pmoA* in cyanobacteria- and moss-dominated biocrust soil in this region (Hu et al., 2019). More CH$_4$ emission events and higher variability were observed during the growing season, especially in wetter 2014 (vs. 2013) (Figs. 3 and 5B) due to more effective rainfall events (Fig. 1). On the one hand, the higher soil moisture in 2014 might reduce gas diffusivity of oxygen and atmospheric CH$_4$ into soil to reach methanotrophs and create anaerobic condition for CH$_4$ production by methanogenesis (Wang et al., 2009). On the other hand, depletion of soil oxygen due to impulses of respiration after rainfall event (Hu et al., 2015a; Zhao et al., 2016) could strengthen soil anaerobic condition that could be in favor of CH$_4$ production (Lafuente et al., 2020). Alternatively, ammonium (NH$_4^+$) can suppress CH$_4$ oxidation in the soil (Jiang et al., 2010) because some of the methanotrophs can switch to oxidizing NH$_4^+$ with increased availability of NH$_4^+$ (Hanson and Hanson, 1996). There is a higher rate of N mineralization and nitrification during the growing season relative to the non-growing season (Hu et al., 2015b), which can supply more NH$_4^+$ during the growing season and thereby inhabit CH$_4$ oxidation. However, considering the dependency of annual accumulative CH$_4$ effluxes on biocrust type (Table 1), there is a need to ascertain distribution and area of different biocrusts in desert region to evaluate GHG budget in drylands.

Soil temperature and moisture could regulate CH$_4$ exchange between soil and atmosphere (Dijkstra et al., 2013; Lin et al., 2015) by changes in gas diffusivity and the activities and abundance of CH$_4$ production and oxidization related microorganisms (Galbally et al., 2008; Lafuente et al., 2020). Thus, how CH$_4$ efflux responds to warming relied on the balance of gas diffusivity and metabolic stress (Luo et al., 2013). Inconsistent with previous reported decreased CH$_4$ uptake in response to warming in semi-arid grasslands (Dijkstra et al., 2013; Lafuente et al., 2020), we found that warming mostly did not affect average CH$_4$ effluxes (Figs. 3 and 5). Perhaps, the indirect drought effects caused by warming and OTC sheltering of precipitation might facilitate atmospheric CH$_4$ diffusion into soil to reach methanotrophs and thereby accelerate CH$_4$ oxidation (Lafuente et al., 2020; Lin et al., 2015) when soils are relatively wet. In contrast, soil drying might limit the activities of methanotrophs in drought soil condition (Galbally et al., 2008). As the result of the combination of these opposing effects, CH$_4$ effluxes were not changed in most cases. However, warming caused a slight increase of annual accumulative CH$_4$ uptake (Table 1) and a significant increased annual average CH$_4$ uptake in 2014 for cyanobacteria-dominated biocrust soil (Fig. 5B), which might be ascribed to higher abundance of *pmoA* under warming and rainfall exclusion conditions (Lafuente et al., 2020). These results imply that the effects of enhanced diffusivity of atmospheric CH$_4$ in warming and drought condition might override the limitation of reduced soil moisture on the activities of methanotrophs in the arid desert biocrust ecosystem, especially in the wetter year. It also highlights that variations in precipitation might play vital roles in determining the response of CH$_4$ efflux to climatic warming in the arid desert biocrust soil.

4.3. N$_2$O emission

Several biological pathways including ammonia oxidation, nitrifier denitrification, heterotrophic denitrification, anaerobic ammonium oxidation and dissimilarity nitrate reduction to ammonium, are known to produce or consume N$_2$O in the soil (Hu et al., 2017; Meyer et al., 2008). Abed et al. (2013) found that incomplete denitrification rather than anammox (anaerobic ammonium oxidation) was the dominant pathway that leads to N$_2$O production in arid desert biocrust soil, with a higher potential rate in cyanobacterial than lichen biocrust. No significant effect of biocrust type on N$_2$O efflux (Figs. 4 and 5) could be largely ascribed to extremely lower rates of denitrification and anammox in the arid deserts (Johnson et al., 2007; Strauss et al., 2012). However, we detected most N$_2$O emission events occurred during the growing season (Fig. 4), which might partially be the result of relatively higher levels of N availability and higher rates of N mineralization and nitrification (Hu et al., 2015b) offering substrates for denitrification. Moreover, wetting-pulse after rainfall events might be beneficial to N$_2$O production via denitrification process due to anaerobic condition created by rainfall and depletion of soil oxygen due to bursts of respiration (Barton et al., 2013; Hu et al., 2015a; Zaady et al., 2013).

A recent study found that warming and drought weakened N transformation rate in moss-dominated biocrust soil by reducing nitrification-related extracellular enzyme activity and gene abundance, whereas it improved nitrification and mineralization rate in cyanobacteria-dominated biocrust soil due to increased abundances of nitrification-related genes in the same region (Hu et al., 2020). In this case, more nitrate substrates in moss-dominated biocrust soil and less substrates in cyanobacteria-dominated biocrust soil for denitrification were expected in the warming condition, which was beneficial to N$_2$O production when soil is wet enough to create anaerobic conditions. This mechanism might be the reason for our observation that warming caused a decreased annual average N$_2$O uptake in cyanobacteria-dominated biocrust soil in 2014 (Fig. 5C). In contrast, warming can also inhibit the denitrification process owing to a more aerobic environment caused by warming-induced drought and OTC sheltering of precipitation. In the drier conditions, fewer soil pores were water-filled and more atmospheric N$_2$O could diffuse into the soil and reach denitrification-related microorganisms (Marusenko et al., 2013), confirmed by the increased N$_2$O uptake in moss-dominated biocrust soil during the growing season in 2014 (Fig. 4B). Probably, cryptogams sustained a longer active duration in the wetter 2014. Moss species might absorb and utilize more inorganic N due to the higher biomass and incapability of N-fixation relatively to cyanobacteria species, thereby reducing nitrate supply for denitrification. In agreement with previous study in arid and semiarid ecosystems (Hart, 2006), our results showed that warming generally did not affect N$_2$O efflux in the desert biocrust soils. These findings do not support the modeling evaluation of increased N$_2$O emission (Xu et al., 2012) and field measurements of reduced accumulative N$_2$O in a semi-arid grassland (Dijkstra et al., 2013) in response to warming. Based on these findings and combined unassociation of N$_2$O with soil temperature and moisture, we speculate that the N$_2$O budget in the arid desert biocrust soil would not be changed in the warmer future.

Previous field measurements have found that Sonoran Desert, Great Basin and Utah soils act as a N$_2$O source with the range from 0.005 to 3.57 μmol N$_2$O-N (Belnap, 2001; Guilbault and Matthias, 1998; Mummey et al., 1994). By contrast, our results showed that biocrust soil acted as a sink of N$_2$O-N at the rate ranging from 0.039 to 0.145 μmol N$_2$O-N mg^{-2} h^{-1}, which was comparable to that (0.09 μmol N$_2$O-N mg^{-2} h^{-1}) in the steppe of Mongolia (Luo et al., 2013) and higher than that in a semi-arid grassland (<0.008 μmol N$_2$O-N mg^{-2} h^{-1}) (Dijkstra et al., 2013). These findings suggest that the arid desert ecosystems might alleviate N limitation and improve soil fertility to a certain extent by uptake of atmospheric N$_2$O, rather than exacerbate the fertility assumed by the previous incubation study in Abed et al. (2013). However, given our low measurement frequency, some wetting-pulses of N$_2$O emission after rainfall events (Zaady et al., 2013) might be missed. It has been estimated that extreme rainfall events lasting for a few hours to several days can contribute up to 80% of

the annual N_2O emissions in drylands (Ussiri and Lal, 2012). Therefore, more continual filed measurements are imperative to accurately estimate N_2O budget in arid desert biocrust soils, especially after rainfall events.

5. Conclusions

Based on our field measurements, we must conclude that there will be a neutral response of GHG effluxes in the arid desert biocrust soils to climatic warming, probably because the direct warming effects on GHGs effluxes might be offset by the indirect effects of drought caused by warming and OTC sheltering of precipitation. In general, there was no statistically significant difference in CO_2, CH_4 and N_2O effluxes between warming and control for three biocrust soils when indirect effects of drought caused by OTC sheltering of precipitation were excluded. However, a marginal reduction in annual accumulative respiratory C release and a slight increase in annual accumulative atmospheric CH_4 and N_2O consumption, especially in moss-dominated biocrust soil, imply that a weak negative feedback to short-term climatic warming could be expected in the arid desert biocrust soil. Therefore, there is a need to ascertain distribution and area of different biocrusts in desert region to accurately evaluate GHG budget in drylands. On the basis of current understanding that the distribution of different types of crusts represents various microclimatic niches, changes that just escape statistical significant can still mean the total area of niches providing for moss biocrust might shrink. Hence, our data can also suggest that this change would contribute more likely than not-significant changes pertaining to ecosystem trace gas effluxes in the long term. Thus, further long term field studies are needed to elucidate this complex of questions, particularly as their answering becomes crucial for the future success of land management options for desert ecosystems.

CRediT authorship contribution statement

Yigang Hu: Conceptualization, Methodology, Software, Writing-Original draft preparation, Supervision. **Bingxin Xu:** Field measurements, Methodology, Software, Data curation. **Yani Wang:** Visualization, Investigation. **Zhenzi He:** Methodology, Software, Validation. **Peng Zhang:** Methodology, Investigation. **Guojie Wang:** Writing- Reviewing and Editing.

Declaration of competing interest

We declare that there are no conflicts of interest. The authors 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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