Effects of freeze-thaw cycles on the soil nutrient balances, infiltration and stability of cyanobacterial soil crusts in northern China

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Abstract

Aims Freeze-thaw fluctuation is a natural phenomenon, which is frequently encountered by biological soil crusts (BSCs) in late autumn and early spring in cold deserts. The objective of our study was to investigate the effects of freeze-thaw cycles (FTCs) on the soil nutrient balances, infiltration and stability of cyanobacterial soil crusts (CSCs) in the temperate desert region.

Methods A controlled incubation experiment was carried out to study the effects of diurnal freeze-thaw cycles (FTCs) on total soil carbon (TC), total soil nitrogen (TN), soil TC/TN, hydraulic conductivity, and strength of light and dark cyanobacterial crusts, respectively. Six successive diurnal FTCs were applied as three temperature regimes (i.e., 6 successive mild FTCs (mild), 6 successive severe FTCs (severe), 3 successive mild FTCs followed by 3 successive severe FTCs (medium)). The experiment intended to simulate natural temperature changes in one of the temperate regions of northern China.

Results Compared with dark CSCs cores, light CSCs cores lost a greater proportion of nitrogen. For both crust cores, Severe FTCs decreased TC and TN more than mild FTCs. However, TC and TN remained relative constant when CSCs cores were treated with severe FTCs after experiencing mild FTCs. TC and TN of both CSCs cores decreased in the earlier FTCs and then remained stable in the later FTCs. TC/TN increased significantly for light CSCs, but only changed slightly for dark CSCs after successive FTCs. The effects of FTCs on the hydraulic conductivity and strength of CSCs were not consistent with our expectations, that FTCs would increase hydrological conductivity and decrease strength. These effects depended on crust type, FTC number and freeze/thaw intensity. Increase in hydraulic conductivity and decrease in strength only occurred in severe treatment in the dark CSCs during the later FTCs.

Conclusions Light CSCs are more sensitive to FTCs than dark CSCs. Mild FTCs decrease less TC and TN than severe FTCs and mostly increase the stability of the CSCs. However, severe FTCs may decrease TC and TN drastically, thereby degrading the BSCs.

Key words: Freeze-thaw cycles · Desert ecosystems· C and N balances · Infiltration · Stabilization

Introduction

Freeze-thaw fluctuation is a natural phenomenon that is frequently encountered by soils in the higher latitude and altitude regions in late autumn and early spring. Climate change is expected to cause milder winters and a thinner and more unstable snow cover in these regions (Cooley 1990), resulting in more frequent freeze-thaw events and increasing depth and severity of soil frost during cold periods (Groffman et al. 2001; Hardy et al. 2001; Mellander et al. 2007). Many studies have conducted to investigate the effects of freezing and thawing on soil characteristics, and suggested that freeze-thaw cycles (FTCs) could alter soil physical properties, microorganisms, carbon and nutrient dynamics, trace gas losses and higher organisms associated with soil (Priemé and Christensen 2001; Oztas and Fayetorbay 2003; Grogan et al. 2004; Henry 2007; Vestgarden and Austnes 2009).

Biological soil crusts (BSCs), whose primary succession stage is cyanobacterial soil crusts (CSCs), consist of cyanobacteria, lichens, mosses, microfungi and bacteria (Belnap 2003a). They are usually distributed in the uppermost soil layer and have distinguished boundaries with soils beneath them (Belnap 2003a). They play a dual role as both constituents of mature arid and semiarid ecosystems, and as pioneers in primary and secondary plant community succession (Belnap 2003a). Their ecosystem functions include stabilizing the soil, fertilizing the soil, changing water regimes, and promoting vascular plants establishment (Eldridge and Greene 1994; Belnap 2003b). Since BSCs are usually located on the uppermost soil profile, they are more likely to be influenced by freeze-thaw events.

Many studies have investigated freezing effects on photoautotrophs in the BSCs, in particular the physiological changes of photoautotrophs (Hawes 1990; Tang and Vincent 1999；Melick and Seppelt 1992; Lin et al. 2004), and few studies were conducted on the whole BSCs, let alone investigated the effects of FTCs on the biogeochemical cycle, water cycle and stability of BSCs. Recently, researches recognize BSCs as a complicated micro ecosystem (Bowker et al. 2010), and those studies based on the population level could not fully represent the characteristics of BSCs. Besides, their biomass is mainly composed of photoautotrophs which can grow and fix carbon or nitrogen in thawing conditions (Belnap 2003b; Tang and Vincent 1999). This makes changes of infiltration and stability, biogeochemical cycles of BSCs during freeze-thaw periods more complicated.

In this study, a controlled incubation experiment was designed to study the effects of diurnal FTCs on the soil nutrient balances, infiltration, and stability of two types of CSCs, i.e., light CSCs (dominated by *Microcoleus*) and dark CSCs (dominated by *Scytonema* and *Nostoc*). We hypothesized that FTCs would increase hydrological conductivity and decrease stability due to their damage to CSCs integrity, and lead to nutrient losses of CSCs. These effects would be aggravated by increasing intensity of freezing and thawing, and dark CSCs were more resistant to FTCs than light CSCs. The experiment was intended to test above hypotheses by simulating natural temperature changes in one of the temperate regions in northern China.

Methods and materials

Site description, crust cores sampling and crust cores preparation

Two sampling sites were located in the central and eastern Kubuq Desert, Inner Mongolia, China (N40°18′, E109°49′, and N40°12′, E110°11′), and samples of light and dark CSCs were collected in the central and eastern site, respectively. Due to its climatic characteristics, freeze-thaw events might occur every month from October to the April of the next year, primarily in October, March and April (Fig. 1). Light CSCs are dominated by the cyanobacterium *Microcoleus*, which first colonizes bare soils and lives 1-4 mm below the soil surface. *Microcoleus* lacks UV protective pigments. During wet periods, it can glide up to the soil surface, while it returns to the depths as soils dry up (Wang et al. 2013). Dark CSCs usually occur in later succession stage after light CSCs (Belnap 2003a). They are dominated by the cyanobacteria *Scytonema* and *Nostoc*, both are small and relatively immobile species. They have a sunscreen pigment in their filament sheaths, which protects them from damage by ultraviolet radiation (Wang et al. 2013).

Samplings were conducted in late October, 2012. For measurements of soil TC and TN changes and crust stability during FTCs, intact CSCs cores of 5cm deep and 5cm in diameter were collected using cutting rings with two end covers (6cm deep, 5cm in diameter). A total of 210 crust cores samples collected. For the measurements of crust infiltration, crust cores (5cm deep, 15cm in diameter) were collected using stainless steel tube with lower cover (6cm deep, 15cm in diameter) (separate 210 crust samples). Those sampling sites were moistened with deionized water prior to coring. To ensure the homogeneity of samples, sampling was carried out within a similar microenvironment where surface microstructure appeared to be similar. After samples were brought to the laboratory, they were watered with 20ml (≈10mm, 5cm deep, 5cm in diameter) and 180ml (≈10mm, 5cm deep, 15cm in diameter) pH-adjusted (pH=7, the average pH in precipitation from 2007-2009) sterile water respectively and photographed after 30 minutes. For both light and dark CSCs, unbroken soil cores were selected and air dried. This was done for samples taken with both the 5cm and 15cm diameter soil cores. These samples were kept in the dark at 10℃until start of treatment.

Freeze-thaw treatment

For each crust type (light CSCs and dark CSCs), the crust cores (3 replicates per FTC per regime) were allocated randomly to three different temperature regimes which were designed according to realistic temperature fluctuation in the sampling sites. Three temperature regimes were defined by an increasing intensity: 6 successive mild FTCs (mild), 3 successive mild FTCs followed by 3 successive severe FTCs (medium), 6 successive severe FTCs (severe) (Fig. 2). For one mild FTC, temperature ranged from -5 to 10℃, while for one severe FTC, temperature ranged from -10 to 5℃. One freeze-thaw cycle was set for 24h with 8h thawing (70μE. $m^{-2}.s^{-1}$) and 16h (dark) freezing. To force the freezing to go from the top to the bottom of the column, as in the field, the columns were placed in blocks of expanded polyester, with holes (5cm deep) fitting the columns (Vestgarden and Austnes 2009). Before the incubation, 19.6 ml (5cm in diameter) and 176.4 ml (15cm in diameter) of pH-adjusted (pH=7, the average pH in precipitation from 2007-2009) water was added by mist sprayer to different sized samples respectively. The addition was slow to prevent the edge effect of water transport along the column walls.

TC and TN measurements

After being used to measure crusts' strength, these cores were ground and used for TC and TN measurements using a C/N analyzer (Flash, EA, 1112 Series, Italy).

Infiltration measurements

Hydraulic conductivity was used as a surrogate measure for crusts' infiltration. It gauges the rate of water movement through soil and accounts for soil's ability to transport water when subject to a hydraulic gradient. Hydraulic conductivity was measured in laboratory conditions on dried samples in stainless steel tubes with lower covers using a Mini Disk Tension Infiltrometer (Decagon Services, Inc., Pullman, WA) with a suction range from 0.5 to 6 cm and a radius of 2.2 cm (Rossi et al. 2012).

The infiltrometer was placed on top of the sample and the height of the water column was measured at equal time intervals as the water penetrated the soil using the graduated cylinder of the instrument. For each sample, hydraulic conductivity was measured at least in triplicate and the mean value recorded.

Stability measurements

A portable needle penetrometer was used to provide an estimate of the surface strength as a surrogate measure for crust stability. Approximately 20 mm^2 surface area was positioned on the crust and gradually applied with pressure applied until the crust failed (Thomas and Dougill 2007). At each sample the measurement was repeated 6 times and the mean value recorded.

Statistics

Two way-repeated measures ANOVAs were used to analyze the effects of crust types and temperature regimes as main factors and FTCs as a within factor on soil TC, soil TN, soil TC/TN, crust hydraulic conductivity and crust strength. The normality of the distribution of the data was tested using the Shapiro-Wilk test. Levene’s test was used to test the homogeneity of variance. When significant interactions were found, one-way ANOVA was used and multiple comparisons for the three temperature regimes within each crust type and each FTC were performed by using least significant difference (LSD test, $P<0.05$). Multiple comparisons were also used for 6 FTCs within each crust type and each temperature regime. All statistical analyses were performed using SPSS 13.0 (SPSS Inc., Chicago, IL).

Results

Changes of soil nutrient of CSCs cores

TC, TN and TC/TN were significantly influenced by crust types, temperature regimes and FTCs (Two-way repeated measure ANOVAs interactions at P<0.001, Table 1).

For light CSCs cores, there were no significant differences of TC between mild and medium regimes throughout the experimental period. For these two regimes, the TC decreased by 0.153 g/kg and about 18.1% compared with the original value after 6 successive FTCs. Meanwhile, the TC decreased by 0.318g/kg and about 37.6% for severe regime. The TC differences between severe with mild and medium regimes occurred after the fourth FTC (S1; Fig. 3a). For dark CSCs cores, there were also no significant differences of TC between both mild and medium regimes throughout the experimental period. For these two regimes, the TC decreased by 0.43 g/kg and about 26.2% compared with the original value after 6 successive FTC while for severe regime it decreased by 0.76g/kg and about 46.3% (S2; Fig. 3b). For both crust types, The TC of crust cores decreased gradually and then remained stable with the increasing FTC numbers in all three temperature regimes (light CSCs: mild, p=0.017, severe, p<0.001, medium, p=0.014; dark CSCs: mild, p<0.001, severe, p<0.001, medium, p<0.001) (S1,2).

For light CSCs cores, there were no differences of TN among three regimes at the end of the experiment (p=0.188). TN decreased by 0.028g/kg, equivalent to 82.5% of the original content after 6 successive FTCs. However, compared with mild and medium regimes, the TN of severe regime reduced rapidly. The content of TN decreased to the lowest level just after 2 FTCs (S1; Fig. 3c). For dark CSCs cores, the TN decreased differently among three regimes at the end of the experiment (p=0.027). These values reduced by 0.025，0.044，0.033g/kg respectively. For severe regime, their TN values were always lower than mild regime during the experiment period, while the values of medium regime were usually between counterpart values of mild and severe regimes after the fourth FTC (S2; Fig. 3d). For both crust types, The TN of crust cores also decreased gradually and then remained stable with the increasing FTC numbers in all three temperature regimes (light CSCs: mild, $p<0.001$, severe, $p<0.001$, medium, $p<0.001$; dark CSCs: mild, $p<0.001$, severe, $p<0.001$, medium, $p<0.001$) (S1,2).

For the TC/TN of light CSCs cores, there were few differences between mild and medium regimes throughout the experimental period. Although there were no differences between three temperature regimes at the end of experiment ($p=0.089$), TC/TN of severe regime increased rapidly than mild and medium regimes. Generally, TC/TN increased and maintained stable with increasing FTC numbers under three different temperature regimes (mild, $p<0.001$, severe, $p<0.001$, medium, $p<0.001$). By going through 6 FTCs, all the ratios of TC to TN increased by about 3.75 times (S1, Fig. 3e). For the TC/TN of dark CSCs cores, there were slightly differences between three temperature regimes throughout the experiment (Fig. 3f). TC/TN fluctuated slightly and no obvious trend was detected after successive FTCs (mild, $p=0.026$, severe, $p<0.001$, medium, $p=0.025$) (S2, Fig. 3f).

Changes of hydraulic conductivity and strength of CSCs

Crust hydraulic conductivity and strength were significantly influenced by crust types, temperature regimes and FTCs (Two-way repeated measure ANOVAs interactions at $P<0.001$, Table 1).

For the hydraulic conductivity of light CSCs, there were no significant differences between mild and medium regimes throughout the experiment. Hydraulic conductivity decreased and then bounced back to the original level in mild and medium regimes (mild, $p<0.001$, medium, $p<0.001$). However, these values reduced and remained steady with increasing FTC numbers in severe regime ($p<0.001$) (S1,

Fig. 4a). For dark CSCs, their hydraulic conductivity did not change significantly through the experiment in mild (p=0.69) and medium (p=0.16) regimes. Compared with mild and medium regimes, the hydraulic conductivity of severe regime first decreased and then increased, and at the end of the experiment their values increased by 37.64% compared with the original level (p<0.001) (S2, Fig. 4b).

For the strength of light CSCs, few differences were found between mild and medium regimes. However, the corresponding values of severe regime were generally lower than mild and medium regimes. Throughout the experiment, strength first increased and then decreased with the increasing FTC numbers in all temperature regimes (mild, p<0.001, severe, p<0.001, medium, p<0.001). At the end of the experiment, these values were no significantly different from the origin level (mild, p=0.05, severe, p=0.07, medium, p=0.39) (S1, Fig. 4c). For dark CSCs, differences between three regimes mainly occurred after the fourth FTC and these corresponding values decreased with intensity of freeze/thaw. Their strength first increased and then decreased with the increasing FTC numbers in mild (p<0.001) and medium (p<0.001) regimes. Comparatively, their strength first increased and then maintained steady in severe regime (p<0.001) (S2, Fig. 4d).

Discussion

Soil nutrient of CSCs cores

During successive FTCs, TC and TN of both light and dark CSCs cores first decreased and then remained stable (S 1, 2; Fig. 3). This result suggests that the amount of carbon and nitrogen release is more than the amount of carbon and nitrogen fixation at the earlier FTCs, and thereafter these amounts are gradually equalizing at the later FTCs. Respiration by microorganisms in and beneath the crust, leads to carbon loss within the crust cores (Garcia-Pichel and Belnap 1996). Denitrification by these microorganisms leads to nitrogen losses within the crust cores (Marusenko et al. 2013). During the earlier FTCs, Microorganisms in the soil in or beneath the crusts received sufficient carbon and nitrogen and became more active after thawing (Schimel et al. 2006). Meanwhile, Carbon and nitrogen fixation were reduced or stopped due to the decrease or restriction of photosynthesis by cyanobacteria during the earlier FTCs period (Wang et al. 2013). With increasing numbers of FTC, carbon and nitrogen release was reduced due to decreased available carbon. For dark CSCs cores, nitrogen fixation might gradually recover with the physiological acclimation of nitrogen fixing cyanobacteria and then N input and loss balanced again at the later stage of the experiment.

Compared with light CSCs cores, dark CSCs cores lose more carbon likely to the atmosphere. Carbon’s vertical distribution in dark crusts might be different from light crusts. Most of the organic carbon of dark CSCs was distributed in the soil surface, which experienced more extreme temperature changes affected by freeze-thaw stress. In addition to differences in carbon distribution, dark CSCs might be thicker than light CSCs with a greater proportion of microbial biomass distributed on the soil surface (Hu et al. 2003). Temperature retention of dark CSCs would be greater than light CSCs. Microorganisms in or beneath the dark CSCs would live in a relatively stable temperature regime. They metabolize more actively than those in or beneath light CSCs and lead to greater carbon losses. For light CSCs cores, TN decreased remarkably after FTCs. Comparatively, a smaller proportion of TN was lost in the dark CSCs cores. This implies that TN content of dark CSCs cores is more resistant to temperature treatments. Previous studies (Delgado-Baquerizo et al. 2013; Reed et al. 2012) have found that N cycle under well-developed BSCs could be more resistant to changes than poor-developed BSCs. The TC/TN of light CSCs cores changed remarkably while for dark CSCs cores TC/TN fluctuated slightly during the process of freezing and thawing. It could be inferred that light CSCs are easily disturbed by FTC and this would lead to decrease in quality of light CSCs. This was also supported by the fact that there were no significant differences between the three regime treatments at the end of the experiment. The results showed that FTC led to a state of nitrogen starvation in light CSCs. The tolerance capacity of these crusts to FTC was consistent with the succession series of CSCs.

Compared with the mild and medium FTCs, severe FTCs decreased the soil TC and TN more for both light and dark CSCs cores. This indicated that more TC and TN were lost by increasing the intensity of freeze/thaw. Small differences between mild and medium FTCs indicated that lower temperature acclimation might reduce the loss of TC and TN of the crusts cores. For medium FTCs, with the slow freezing rate, cyanobacteria would have enough time to adjust their physiological processes and receive less damage than severe temperature treatment. The freezing point for soil cyanobacteria is usually below -5℃ (Lin et al. 2004). For severe freezing, the liquid water in the cyanobacterial cells might freeze and cause cells to crack and release more materials from cells. Hence, more damage to cyanobacteria occurred in severe FTCs treatment. However, cyanobacteria evolved a series of thermal adaptations and acclimations for cold environments, including maintenance of membrane fluidity, molecular adaptation of enzymes to compensate for the reduction of chemical reaction rates at freezing, and adaptation and acclimation of the photosynthetic electron transport and the energy balance (Tang and Vincent 1999; Tamaru et al. 2005; Morgan-Kiss et al. 2006).

Compared with the effects of trampling disturbance (Barger et al. 2006), a greater proportion of carbon and nitrogen was lost by FTCs in this study. For example, it was reported that there were only 1% reduction and 1-3% reduction after trampling for the TC and TN of CSCs, respectively (Barger et al. 2006). The large difference in TC and TN loss might be a result from using a different CSC model. Barger et al. measured the TC and TN of total CSCs rather than CSCs cores. It is supposed that this enormous loss might be related to the death of CSC organisms induced by FTCs and then carbon and nitrogen were released by microbial respiration (Maestre et al. 2013) and denitrification. As a result, more work examining the biogeochemical process of CSCs would be needed, especially identifying changes during winter in the temperate regions. Compared with the soils of agricultural or forest environment, freezing and thawing also gave rise to much greater losses of TC and TN for CSCs (Matzner and Borken 2008; Vestgarden and Austnes 2009). The reason for this might be related to the presence of large amounts of mineralizable C in BSCs, especially in higher moisture conditions for CSCs (Miralles et al. 2013).

Infiltration and stability of CSCs

Infiltration and strength of BSCs are influenced by many factors, such as texture, phototrophic abundance, microbial composition, exopolysaccharides (EPS) content, and crust thickness (Warren 2001; Belnap 2006). Freezing and thawing might increase the thickness of crusts, which would result in decreased infiltration, and an increase in strength for CSCs in sandy soils (Xie et al. 2007). Meanwhile, FTCs decreased the microbial biomass, which might cause increase of infiltration and decrease of strength (Xie et al. 2007). Alternatively, it might destroy the microstructure of EPS, which results in a decrease of infiltration and an increase in the crust strength (Rossi et al. 2012). Our results reveal that these effects depend on crust type, FTC numbers and freeze/thaw intensity. Only the severe treatment, during later

FTCs, led to hydraulic conductivity increases and strength decreases. This finding highlights the challenges in predicting the effects of freezing and thawing on the infiltration and stability of CSCs.

FTCs, climate change, succession and degradation of CSCs

Mild FTCs slightly decreased the soil TC and TN, decreased or did not change the infiltration and increased or did not change the stability of CSCs. This implies that moderate FTCs may suppress the dominant crust species and provide more niches for new species to occupy within the crusts. Therefore, mild FTCs may promote the succession of BSCs. However, severe FTCs drastically decreased the soil TC and TN of CSCs cores, and sometimes increased the infiltration and decreased the stability of CSCs, implying that severe FTCs may degrade the BSCs. Presumably, increasing precipitation and temperature in the region (Piao et al. 2010) may result in more frequent freeze-thaw events. Consequently, more carbon and nitrogen loss would be expected in the future and would accelerate the degeneration of BSCs in the arid and semiarid ecosystems (Maestre et al. 2013). In addition, our results support the conclusion that low temperature acclimation by BSCs would reduce the loss of carbon and nitrogen of crusts. However, with more extreme weather patterns, acclimation by BSCs may be slow, leading to long-term detriments to the BSCs.

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Table 1 Results of two-way repeated measure ANOVAs with crust types (CT) and temperature regimes (TR) as main factors (between subject) and freeze-thaw cycles (FTCs) as a within subject over the experimental period on total carbon (TC), total nitrogen (TN), ratio of total carbon to nitrogen (TC/TN) of crust cores, and crust hydraulic conductivity (HC) and strength (CS).

Source of variation	TC			TN		TC/TN		HC		CS	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Between-subject											
CT	1	644	<0.001	2271	<0.001	4665	<0.001	1533	<0.001	1144	<0.001
TR	2	9.1	0.004	9.0	0.004	32.0	<0.001	10.2	0.003	54.3	<0.001
CT×TR	2	3.1	ns	2.6	ns	34.4	<0.001	11.6	0.002	20.9	<0.001
Within-subject											
FTCs	5	352	<0.001	704	<0.001	231	<0.001	38.2	<0.001	52.4	<0.001
FTCs× CT	5	70	<0.001	16.8	<0.001	231	<0.001	29.7	<0.001	11.5	<0.001
FTCs×TR	10	14.2	<0.001	8.4	<0.001	23.7	<0.001	5.7	<0.001	20.0	<0.001
FTCs×CT×TR	10	3.6	<0.001	4.3	<0.001	22.3	<0.001	10.8	<0.001	16.0	<0.001

Captions

Fig 1. Monthly maximum and minimum air temperature (line) and monthly precipitation (column) averaged from 1978 to 2010 in the study site. The bar above the column indicates the highest precipitation record of each month.

Fig 2. Light intensity, temperatures and times of sampling (thin arrows) for the three regimes: (A) light intensity; (B) mild regime: six successive mild FTCs; (C) severe regime: six successive severe FTCs; (D) medium regime: three successive mild FTCs and successive severe FTCs.

Fig 3. TC, TN and TC/TN changes (Mean±SD) with increasing FTC numbers in three temperature regimes for light and dark cyanobacteria crust cores respectively. Different letters within the same times indicate a significant difference at $P < 0.05$.

Fig 4. Hydraulic conductivity and strength changes (Mean±SD) with increasing FTC numbers in three temperature regimes for light and dark cyanobacteria crusts respectively. Different letters within the same times indicate a significant difference at $P < 0.05$.

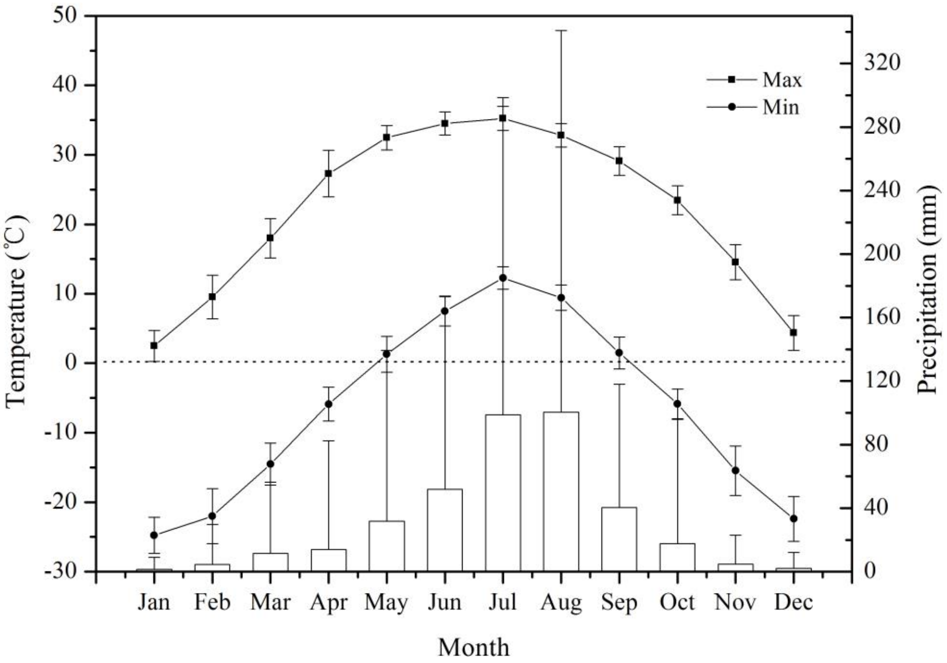
Max
Min
Temperature (℃)
50
40
30
20
10
0
-10
-20
-30
Precipitation (mm)
320
280
240
200
160
120
80
40
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Fig 1

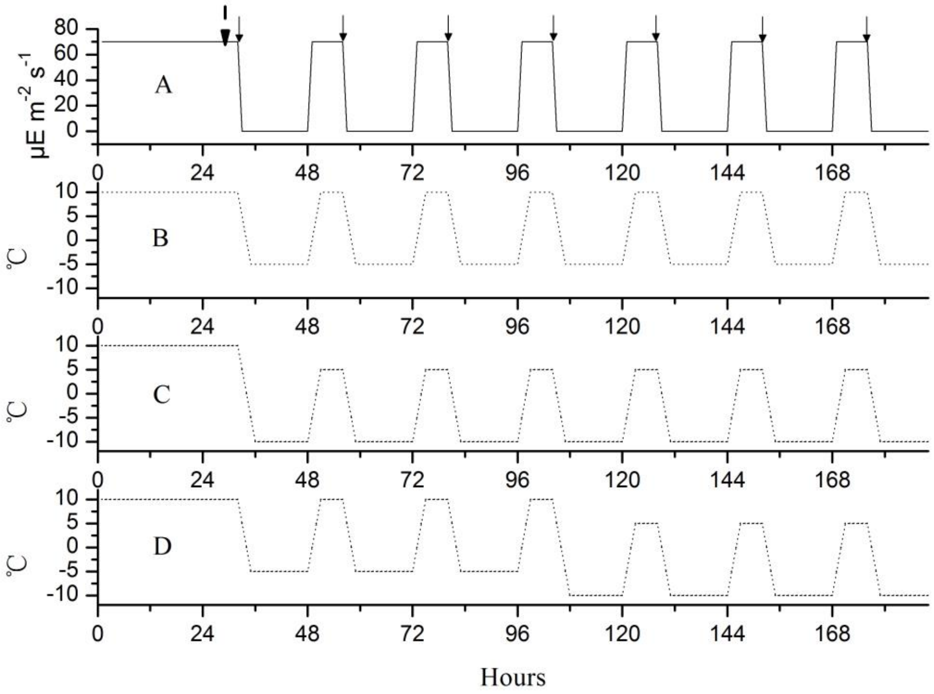

Fig 2

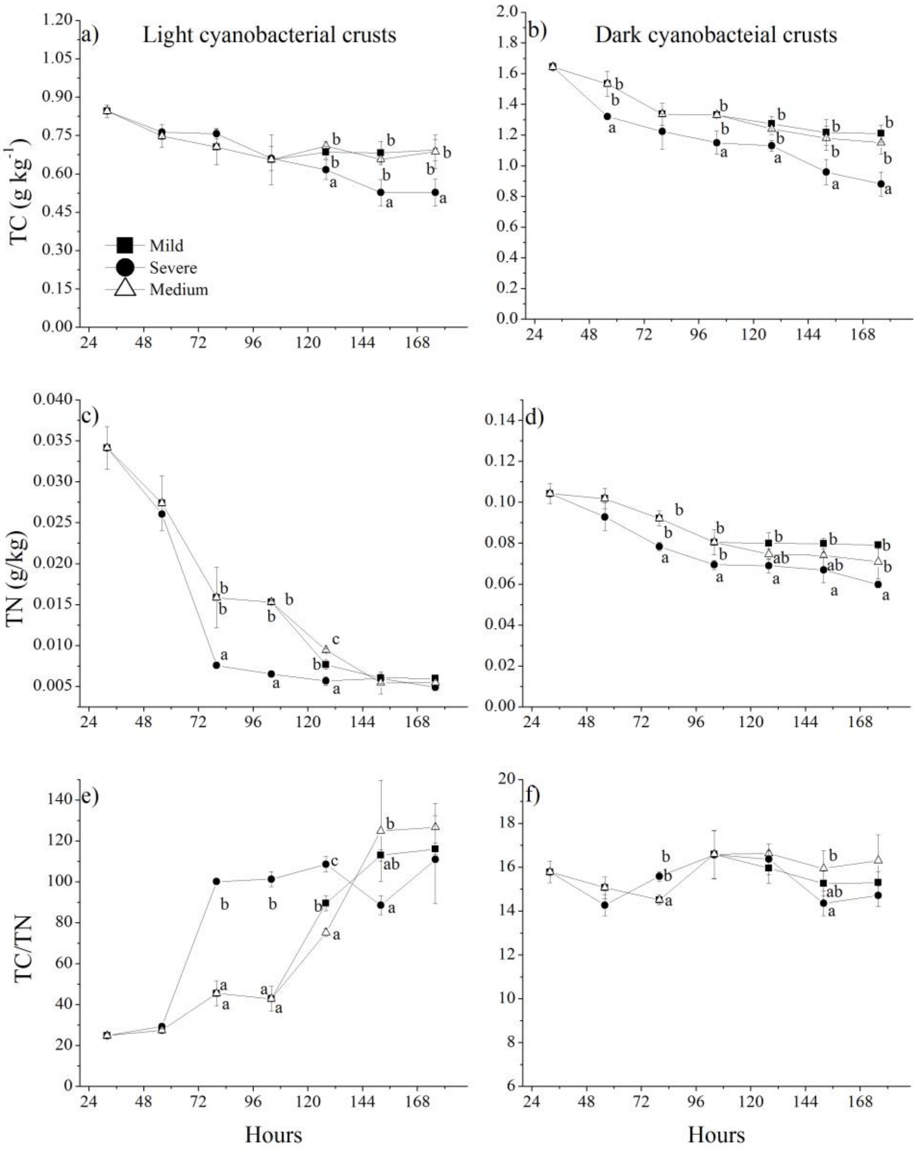
a)
Light cyanobacterial crusts
b)
Dark cyanobacteial crusts
c)
d)
e)
f)
TC (g kg^{-1})
TN (g/kg)
TC/TN
Hours
Hours
Mild
Severe
Medium
0.00
0.15
0.30
0.45
0.60
0.75
0.90
1.05
1.20
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
0.005
0.010
0.015
0.020
0.025
0.030
0.035
0.040
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0
20
40
60
80
100
120
140
6
8
10
12
14
16
18
20
24
48
72
96
120
144
168

Fig 3

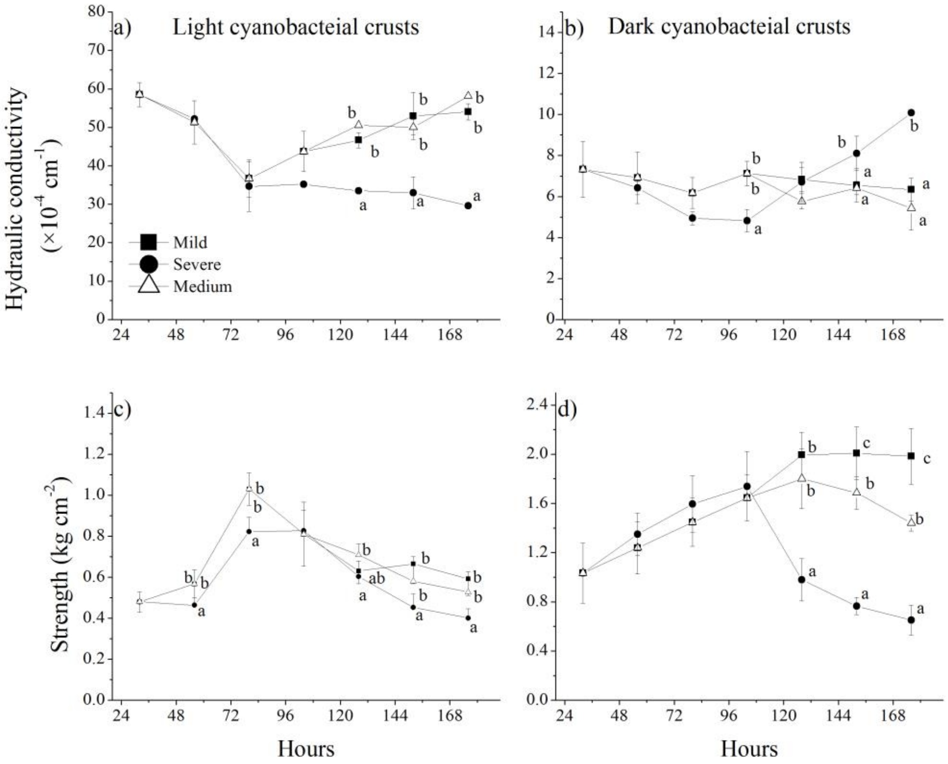
a) Light cyanobacteial crusts
b) Dark cyanobacteial crusts
c)
d)
Hydraulic conductivity ($\times 10^{-4}$ cm^{-1})
Strength (kg cm^{-2})
Hours
Mild
Severe
Medium
0
10
20
30
40
50
60
70
80
2
4
6
8
10
12
14
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
2.0
2.4
24
48
72
96
120
144
168
a
b
ab
c

Fig 4