GRÓ Land Restoration Training Programme
Árleynir 22, 112 Reykjavik, Iceland

Final project 2022

RESPIRATORY RESPONSES OF A SUBARCTIC BIOCRUST FROM THE HIGHLANDS OF ICELAND TO EXPERIMENTAL WARMING: COMPARISON BETWEEN A DRY AND A WET SUMMER

Gideon Asamoah
CSIR-Soil Research Institute
Academy Post Office
Kwadaso, Kumasi, Ghana
gasamoah97@yahoomail.com

Supervisor
Dr Alejandro Salazar Villegas
Agricultural University of Iceland
alejandro@lbhi.is

ABSTRACT

Understanding the response of biocrust respiration to warming is crucial for terrestrial carbon cycle simulation in high north ecosystems. Biocrust respiration is sensitive to warming which could result in positive carbon-climate feedback. However, evidence on the sensitivity of biocrust respiration to warming is mostly from arid and semi-arid ecosystems. To assess how subarctic biocrust responds to warming, a field experiment was undertaken to study the effect of experimental warming on the respiratory responses of subarctic biocrust under different soil moisture conditions. Warming plots simulated by using Open Top Chambers (OTCs), and plots of ambient environment (control) were established. A LICOR-6400 and an EGM-5 portable gas analyser were used to measure soil respiration rates in June of two different years, 2019 and 2022, corresponding to dry and wet moisture conditions respectively. Soil moisture and temperature were also measured from the plots, simultaneously with soil respiration, using probes attached to the portable gas analysers. There was no effect of warming on soil moisture content under the different moisture conditions of dry and wet. Soil temperature increased by 1.2°C, corresponding to a 9.8% increase in the OTCs in relation to the control plots only under drier conditions. Under wet conditions, warming had no effect on the soil respiration rate. However, the effect of warming on soil respiration rate was negative under drier conditions. The results of this study showed that the effects of warming on the respiration of subarctic biocrust largely depends on moisture conditions.

Key words: Subarctic biocrust, respiration, warming. moisture conditions

This paper should be cited as:

Asamoah G (2022) Respiratory responses of a subarctic biocrust from the highlands of Iceland to experimental warming: Comparison between a dry and a wet summer. GRÓ Land Restoration Training Programme [Final project]
https://www.grocentre.is/static/gro/publication/850/document/asamoah2022.pdf

TABLE OF CONTENTS

1. INTRODUCTION

1.1 Background

Biological soil crusts (biocrusts) are skin-like systems that form on the surface of soil in areas where vascular plants are limited due to harsh environmental conditions (Belnap et al. 2016), such as hot and cold desserts, alpine habitats and polar regions (Weber et al. 2022). They comprise photosynthetic and diazotrophic communities of bacteria, fungi, algae, lichens and mosses that colonize the top layers of the soil (Belnap et al. 2016) and cover ca. 12% and 30% of terrestrial and dryland ecosystems, respectively (Rodriguez-Caballero et al. 2018).

Due to the ability of biocrusts to regulate biogeochemical processes, such as nutrient and water cycles (Delgado-Baquerizo et al. 2015), and to increase soil fertility (Belnap et al. 2016), they are often considered as engineers of the ecosystem (Moreno-Jiménez et al. 2020). Organisms such as vascular plants, nematodes and microarthropods usually benefit from the key ecosystem functions provided by biocrusts for their establishment and performance (Jones et al. 1997).

In many ecosystems, biocrust is a primary fixer of carbon (C) and nitrogen (N) (Rodriguez-Caballero et al. 2018; Sancho et al. 2016). Biocrusts contribute substantial amounts of nitrogen (N) through biological N fixation (Stewart et al. 2011) in N-limited biomes such as arctic tundra through the activities of lichens (Rousk et al. 2017) and cyanobacteria (Pietrasiak et al. 2013), which transfer readily available N to underlying soils (Nevins et al. 2020). The C and N inputs into ecosystems by biocrust leads to the abundance of microbes involved in processes such as nitrification and denitrification in the root zone of plants (Cheng et al. 2021; Dias et al. 2020).

Biocrusts play a key role in mediating C cycles by sequestering CO_2 from the atmosphere (Duran et al. 2021) and breaking down of organic residues (Porada et al. 2013). Globally, cryptogrammic covers, including biocrusts, rock crusts and moss carpets, fix around 14.3 Gt CO_2 per annum, corresponding to 3.9 Gt C at the global scale and about 7% of the net primary productivity by terrestrial vegetation (Elbert et al. 2012). While biocrusts sequester C, some communities dominated by lichens emit about 40% of C annually in semiarid ecosystems via respiration (Castillo-Monroy et al. 2011). In a revegetated temperate desert, communities of biocrusts mostly dominated by cyanobacteria and algae were found to release 60% of C annually during the growing season (Zhang et al. 2013).

Several factors influence the presence of biocrust and its ecosystem functions. Among these factors, climate strongly influences the type of biocrust present, including in tundra environments (Williams et al. 2016; Bowker et al. 2016). Moisture availability influences the composition and abundance of biocrust, with higher moisture being required for the development of moss-crusts than for cyanobacteria- and lichen-crusts (Borchhardt et al. 2017). The metabolic activities of biocrusts can shut down during dry seasons, but they reactivate in response when water becomes available (Coe et al. 2012).

Projected warming (IPCC 2022) will affect ecosystem functioning in many ways (Berdugo et al. 2020). One of the intrinsic characteristics of biocrusts is their capacity to tolerate and even thrive in extreme environmental conditions (Pointing & Belnap 2012). However, climate change will have a serious effect on biocrust, as the global biocrust cover is projected to decrease by 25-40% under all Representative Concentration Pathways (RCPs) by 2070 (Rodriguez-Caballero et al. 2018). Furthermore, research predicts that climate change will impact significantly on biocrust communities (Zelikova et al. 2012) as well as their associated C cycling (Darrouzet-Nardi et al. 2015; Darrouzet-Nardi et al. 2018).

As an important pathway for modulating C between land and the atmosphere, soil respiration resulting from the breakdown of organic matter by plants and microbes is sensitive to environmental factors, such as temperature and moisture (Zhang et al. 2015). With environmental warming, soil respiration will be greatly impacted (Bond-Lamberty & Thomson 2010).

Studies on climate change impact on biocrust composition and its associated ecosystem functions have been mostly carried out in dry areas of the hot arid and semiarid regions (Guan et al. 2021; Maestre et al. 2013). Biocrust also exists in the cold climates of the polar and high elevation regions (Weber et al. 2022), and in these regions it may respond differently to climate change. Experimental research on cold-adapted biocrust is still scarce and hence this study is carried out to investigate the effect of experimental warming on soil respiration in a cold and mesic subarctic ecosystem dominated (ca. 50% cover) by liverwort (*Anthelia juratzkana*) biocrust in southern Iceland.

1.2 Goals and objectives

The overall goal of this study was to evaluate the potential impact of climate change on respiration rates in a subarctic biocrust.

The specific objectives were to:

1. Determine the influence of warming (ca. +1°C) on inter-annual respiration rates in a subarctic biocrust under dry and wet conditions.
2. Determine the relationships between moisture, temperature and respiration in a subarctic biocrust in the highlands of Iceland, by comparing inter-annual observations under dry and wet conditions.

2. METHODS

2.1 Study area

The study was carried out at the Climate Research Unit at Subarctic Temperatures (CRUST) experimental site (Fig. 1), near Landmannahellir (64°02' N, 19°13' W; 590 m a.s.l.), in the South of Iceland. The experiment was launched by Alejandro Salazar and Ólafur Andrésson in Landmannahellir in 2018 (Salazar et al. 2022). The location has a mean annual temperature of ca. 5°C and mean annual precipitation of 1500 mm (Salazar et al. 2022). Liverwort-based biocrust dominates the surface cover of the area (ca. 50%), followed by mosses (ca. 30%) and *Salix herbacea* dwarf willow (ca. 20%) on an Andosol/Vitrisol substratum (Salazar et al. 2022).

2.2 Experimental design

At the CRUST experimental site, Control (ambient temperature) and Warmed plots (ca. +1°C) were set up and replicated in eight different blocks. The blocks are separated at least 10 m from each other and, within each block, the Control and Warmed plots were separated by a 1-2 m gap. Warming is simulated using Open Top Chambers (OTCs; Marion et al. 1997), according to the protocols of the International Tundra Experiment (ITEX; Henry & Molau 1997). The Control plots had a dimension of 1.5 x 1.5 m. The OTCs, made of transparent polycarbonate, cover a similar area and create an enclosure of about 0.5 m in height.

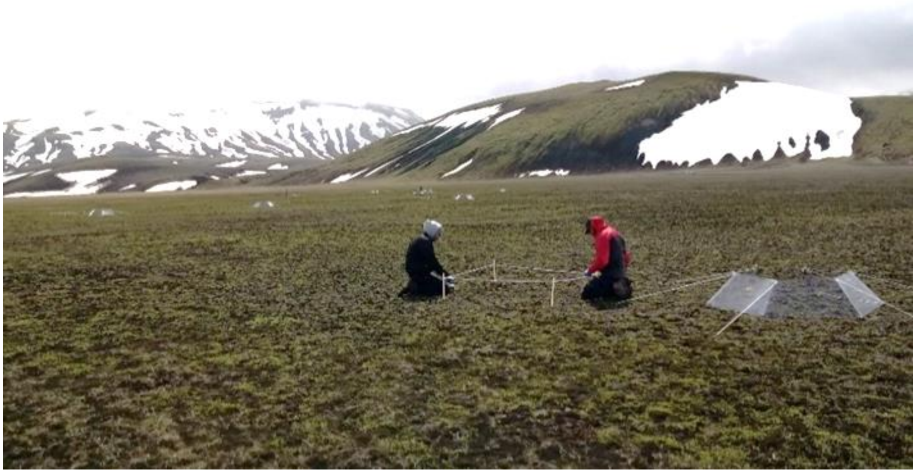


Figure 1. The Climate Research Unit at Subarctic Temperatures (CRUST) experimental site.

Data for two distinct soil moisture conditions, Wet and Dry, were used for this study (Fig. 2). The data for the Wet condition were collected in June 2019 by other team members of the CRUST experiment. I helped collect the data for the Dry condition in June 2022. To measure environmental parameters, such as soil temperature and moisture, loggers were programmed and installed in the field in June 2018. Biocrust respiration, soil temperature and moisture were measured once per year with Infra-Red Gas Analysers (IRGAS), but temperature and moisture were also measured all year round using temperature and moisture sensors.

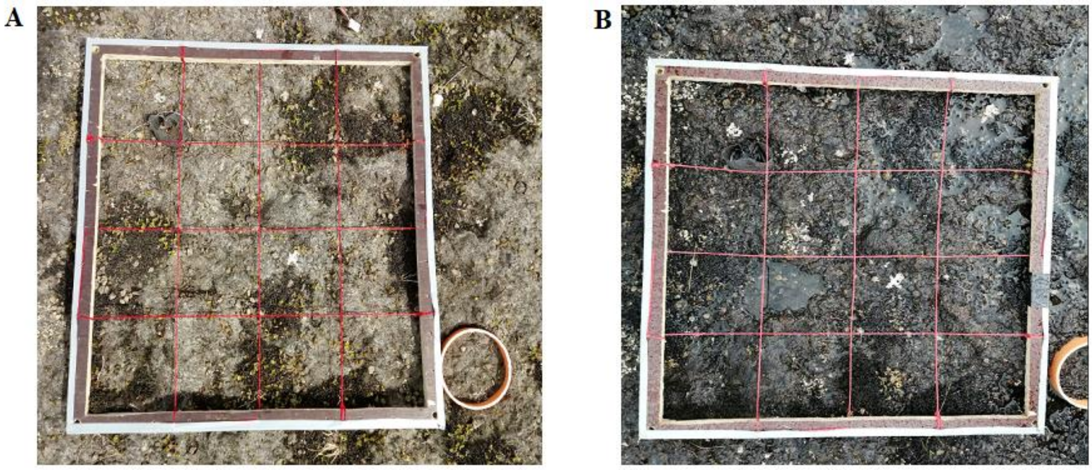


Figure 2. Field conditions in the Dry (A) and Wet (B) summers of June 2019 and 2022, respectively. (Photos: A.V. Salazar, June 2019 and 2022).

2.3 Measurement of biocrust respiration

Measurement of biocrust respiration was carried out using LI-6400 (LI-COR Biosciences UK Ltd) and EGM-5 (PP Systems) portable gas analysers, using an SRC-2 closed dynamic chamber. The LICOR-6400 and EGM-5 were used to measure biocrust respiration in June 2019 and June 2022, respectively. During the measurement, an SRC-2 chamber was firmly placed on the surface for gas flow and accumulation in the headspace of the chamber where an infrared gas analyser (IRGA) measured CO_2 concentration over time. The principle behind EGM-5's operation is the absorption of infrared radiation by CO_2 and the measurement of CO_2 molecule absorption band by a nondispersive infrared (NDIR) sensor in the EGM-5 chamber at a wavelength of 4.25 µm (Tóth et al. 2020). In the field, soil respiration was measured in the Warmed and Control plots in a pairwise manner.

2.4 Measurement of environmental variables

Soil temperature and soil moisture were measured at 0-5 cm depth at the CRUST experiment using the Hydra Probe II (Stevens Water Monitoring Systems, Inc.) attached to the EGM-5 portable gas analyser. Moreover, HOBO U23 Pro v2 Temp/RH and TMC20-HD sensors (Onset Corp., Pocasset, MA, USA) were used to record soil temperatures throughout the entire periods July 2018-June 2019 and July 2021-June 2022 (Appendix I). The sensor loggers were programmed to record the soil temperature every 2 hours.

2.5 Statistical analysis

For data analysis, I used a mixed effect model including the fixed effect of the warming treatment and the random effect of the blocks. The lmer function from the lme4 package was used for this (Bates et al., 2015). Tukey HSD was used for means separation at $p \leq 0.05$ where significant effects of treatments were observed. A linear regression analysis was carried out to determine the relationship between soil respiration and the measured environmental parameters, using the lm function. For all analyses, I used R statistical software version 4.1.2 (R-core-Team, 2020).

3. RESULTS

3.1 Treatment effects on soil temperature, moisture and respiration

Experimental warming increased soil temperature by 0.8°C, or from 11.94±1.02°C to 12.74±1.36°C (Figure 3A; $p = 0.025$). During Dry conditions, soil temperature was significantly increased ($p = 0.09$) by warming but was not affected under Wet conditions (Fig. 3B). Mean soil temperature of 13.53 ±1.26°C and 12.32±1.15°C was recorded for the Warming and Control plots respectively in the Dry regime. In the Wet regime, the mean soil temperature was 11.68±0.52 and11.43±0.54°C in the Warming and Control plots respectively. Warming increased the soil temperature by 1.2°C in the Dry condition.

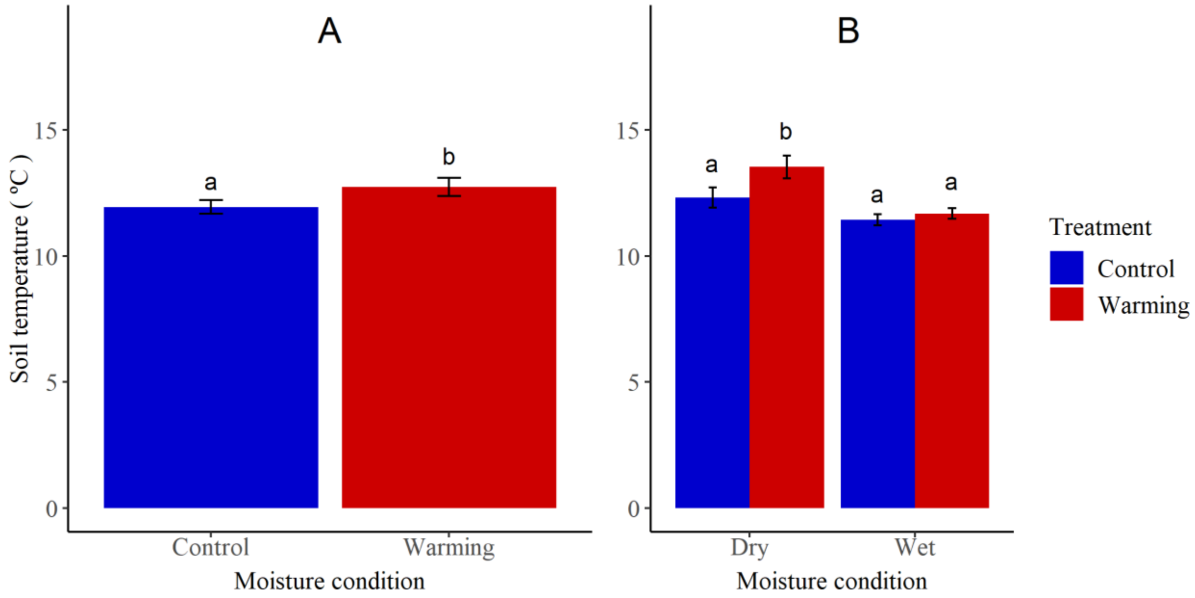


Figure 3. Effects of warming on overall soil temperature (0-5 cm) (A), and soil temperature in the Warming and Control plots under Dry (June 2019) and Wet (June 2022) conditions (B). Error bars with the same letters are not significantly different.

The overall mean soil moisture in the Warming and Control plots were 0.31±0.26 and 0.34±0.25 m^3/m^3 respectively. There was no significant effect of the warming treatment on soil moisture (Fig. 4A; $p > 0.05$). Irrespective of the soil moisture condition, the Warming treatment had no significant effect on soil moisture content (Figure 4B; $p > 0.05$). However, soil moisture content was significantly higher during the Wet conditions (June 2022) than during the Dry conditions in June 2019 (Appendix II; $p < 0.001$). The average soil moisture content in the Dry and Wet moisture conditions was 0.06±0.03 and 0.54±0.05 m^3/m^3 respectively.

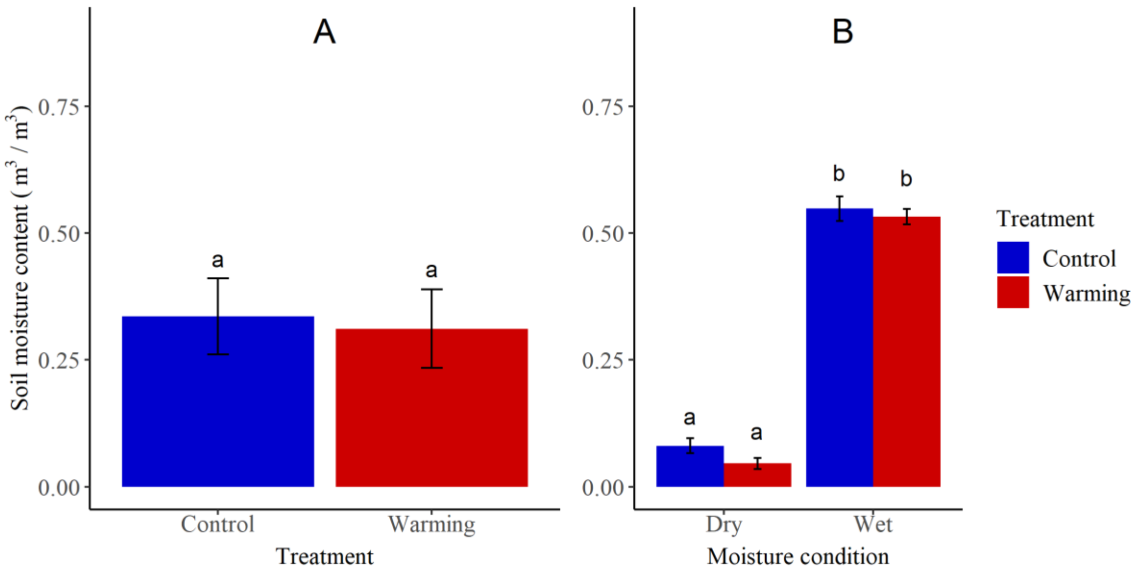


Figure 4. Effects of warming on overall soil moisture (0-5 cm) (A) and moisture content in the Warming and Control plots under Dry (June 2019) and Wet (June 2022) conditions (B). Error bars with the same letters are not significantly different.

Mean biocrust respiration in the Control and Warming plots from all measurements was 0.56±0.513 and 0.52±0.407 µmolCO_2/m^2s respectively. The warming treatment had a significant negative effect on biocrust respiration rate (Fig. 6A; $p < 0.01$). In relation to the Control plots, warming reduced biocrust respiration by 6.8%. However, this negative effect of warming on respiration was only observed in the dry summer of 2019 (Fig. 5B; $p < 0.01$). In the wet summer of 2022, warming did not have any effect on biocrust respiration (Fig. 5B). The Warming plots had a mean respiration rate of 0.856±0.085 µmolCO_2/m^2s and the Control, 1.001±0.189 µmolCO_2/m^2s during the Dry conditions. In the Wet conditions, mean respiration rates of 0.077±0.058 and 0.047±0.021 µmolCO_2/m^2s were measured in the Warming and Control plots respectively. Under drier conditions, warming reduced thebiocrust respiration rate by 14.5%.

Varied responses were observed for the biocrust respiration rate with respect to the two different moisture conditions (Appendix III). Under the Dry moisture content of 6.3% v/v, biocrust respiration rate was highest (0.924±0.156 µmolCO_2/m^2s) and was significantly different ($p < 0.001$) from a respiration rate of 0.061±0.044 µmolCO_2/m^2s under the Wet moisture condition of 54% v/v. Under wet soil conditions, soil respiration rate was reduced by 93% in comparison with drier conditions.

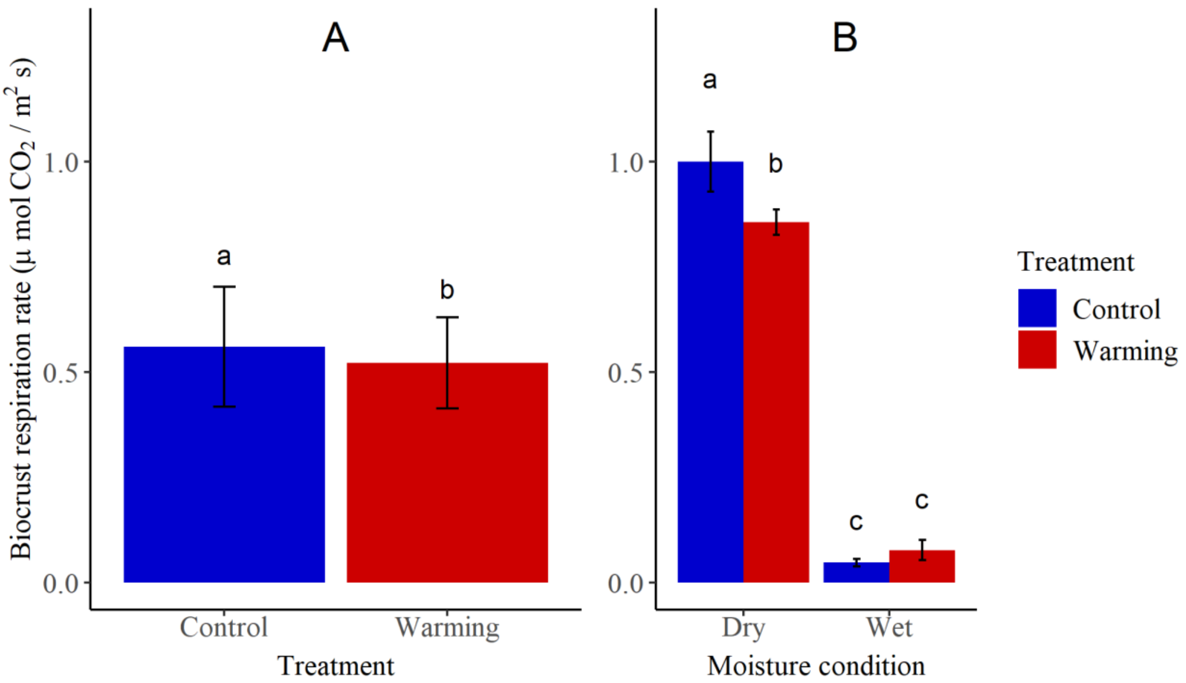


Figure 5. Effects of warming on overall biocrust respiration (0-5 cm) (A) and biocrust respiration in the Warming and Control plots under Dry (June 2019) and Wet (June 2022) conditions (B). Error bars with the same letters are not significantly different.

3.2 Relationship of soil moisture and soil temperature with biocrust respiration

When analysed in the range of moisture conditions between 6.3 and 54%, which includes all the soil moisture recordings during the 2019 and 2022 field campaigns used in this study, biocrust respiration was negatively correlated with moisture (Fig. 7; $R^2 = 0.904$, $p < 0.01$). In this regression analysis, soil moisture accounted for approximately 90% of the variations in the biocrust respiration rate.

Similarly, when analysed in the temperature range 10-16°C, which includes all the soil temperatures recorded during the 2019 and 2022 field campaigns used in this study, biocrust respiration was positively correlated with temperature (Fig. 8; $R^2 = 0.30$; $p = 0.002$). Soil temperature accounted for approximately 30% of the variation in biocrust respiration in this regression analysis.

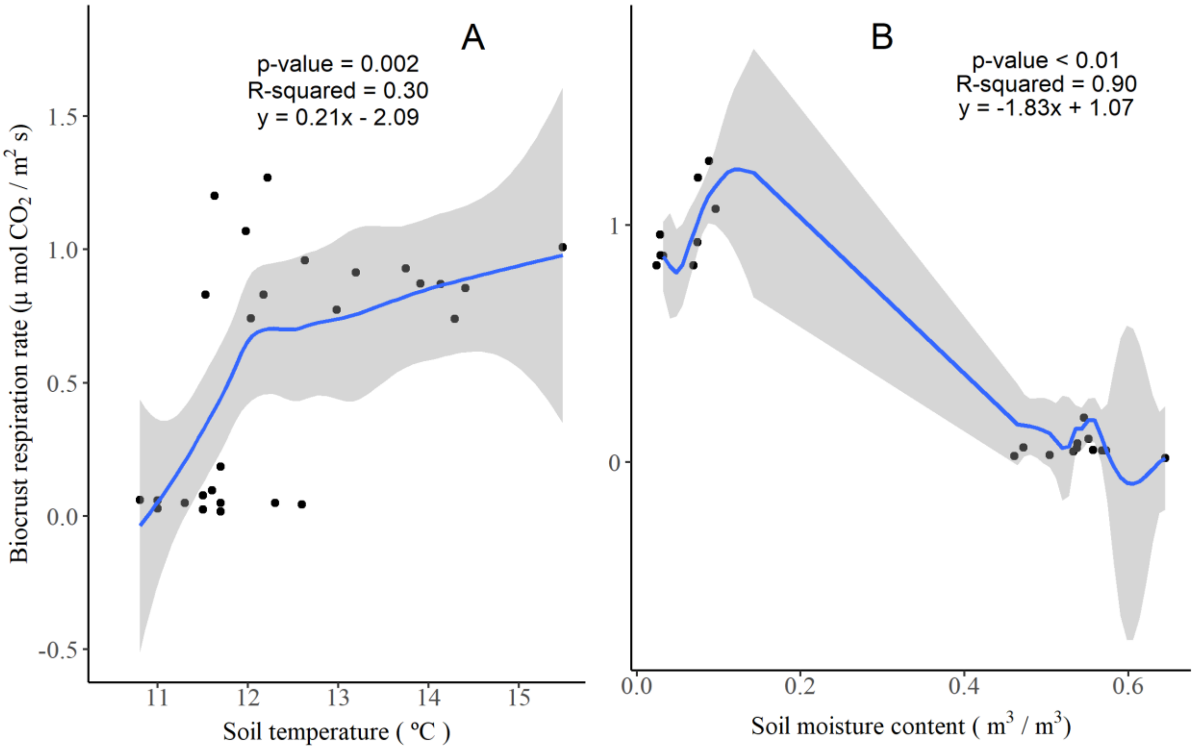


Figure 6. Relationship of biocrust respiration rate with soil temperature (A) and soil moisture (B).

4. DISCUSSION

In this study, warming increased soil temperature by 0.8ºC when both dry and wet years are considered together. However, the effect of warming was not significant for soil temperature under wet moisture conditions but warming increased soil temperature by 1.2ºC under the dry moisture conditions (Fig. 5B). These results suggest that the OTCs were effective in increasing the soil temperatures only during dry conditions. The increase in soil temperature of 1.2ºC by the OTCs is similar to the increase in global mean annual temperature for the last century as well as to the increase predicted for the coming decade (IPCC 2022).

Warming did not affect soil temperature during wet conditions, possibly because the sky was cloudy at the time of measuring respiration, so there was less light coming into the OTCs and therefore less chance for the OTCs to warm up the soil, This, in turn, is probably because the available heat goes into evaporating soil moisture (latent heat) instead of warming the soil (latent heat). When comparing both years, soil temperature was positively correlated to respiration ($p = 0.002$; $R^2 = 0.30$; Fig. 8). The relationship between soil temperature and respiration rate is nonlinear as the soil respiration increases with increasing soil temperature (Kirschbaum 1995) up to a certain point and then starts to decrease with further increase in temperature. At the extreme ends of the soil moisture and temperature spectra, soil respiration declines (Rustad et al. 2001; Davidson et al. 2006). This is due to a reduction in microbial activity resulting from the lack of optimum conditions for the metabolic activity of biocrusts.

Warming had no significant effect on soil moisture under either wet or dry conditions (Fig. 4). Although OTCs usually reduce soil moisture, this is generally not the case in surface soil (0-5 cm), mainly in the tundra biome in the high north (Salazar et al. 2020). Warming has the tendency to increase evapotranspiration but the input of water into the soil through precipitation and/or snow melting could be much higher, resulting in no difference between the Control and OTC plots. In this study, soil moisture content negatively correlated with soil respiration ($p < 0.05$; $R^2 = 0.90$). This does not, however, indicate that an extremely low soil moisture level will result in high respiration rates. The soil respiration rate is low at low moisture levels and then increases with increasing moisture content up to optimum levels; it then decreases with further increases in soil moisture when the soil is saturated with water (USDA 2014). Under dry soil conditions, respiration is impeded due to the reduction in solute transport through the soil which may force soil microbes into dormancy (Manzoni et al. 2014). Conversely, high moisture conditions restrain soil respiration by suppressing oxygen supply from the atmosphere (Moyano et al. 2013) creating an anaerobic condition that limits the breakdown of organic matter. In this study, soil respiration was significantly higher in Dry conditions than in Wet conditions (Appendix III). Biocrusts have the tendency to survive and expand spatially under harsh environmental conditions of low soil moisture content (Jia et al. 2019). However, under saturated soil conditions, such as those of the Wet period, metabolic activities of organisms are reduced due to the soil pores filling up with water. This creates an anoxic environment that is unfavourable to aerobic microbes (Unger et al. 2009) and thus inhibits the respiration of soil microbes. This is likely what happened during the Wet conditions in this study, since the biocrust surface was saturated with water (Fig. 2). Biocrusts swell upon wetting and reduce the available soil pore spaces for water infiltration (Fischer et al. 2010). The effect of this is mostly exhibited on sandy soils with large pores and hydraulic conductivity (Warren 2001). This could explain why, under the Wet conditions, the soil surface was completely flooded with water, but the soil moisture content was 54%.

Warming can increase (Escolar et al. 2015) or decrease (Fang et al. 2018) biocrust respiration. In the present study, warming decreased biocrust respiration at *Anthelia* biocrust-dominated sites only under dry conditions (Figure 6). Warming has been found to induce drought that inhibit microbial activity thus limiting biocrust respiration under decreased levels of moisture (Fang et al. 2017). Although warming did not seem to have a significant effect on soil moisture, the observed negative effect of warming on the soil respiration rate might be due to increased soil temperatures (Figure 5) which reduce carbon use efficiency (Li et al. 2019) as warming suppresses microbial growth by raising the energy cost of maintaining existing biomass (Sinsabaugh et al. 2013). The differences in soil respiration between the control and OTC plots in the dry year could have been related to warming-induced differences in the successional state of the biocrust (Tucker et al. 2019). Moreover, in an alpine meadow of the Qinghai-Tibetan Plateau, warming chnaged respiration from a negative to positive feedback under dry and wet periods respectively (Quan et al. 2019). In a similar study, warming was found to have a negative effect on soil respiration under drier conditions (Peng et al. 2015).

Warming has previously been found to have a more positive effect on soil respiration in wet years than in dry years (Escolar et al. 2015). In a study by Escolar et al. (2015), warming increased soil temperature by ca. 2.4^{o}C which could account for the differences in observation between their study and the current study. Furthermore, soil respiration was measured monthly in the study by Escolar et al., whereas in the current study, soil respiration was only measured once a year during the month of June. Soil respiration has been found to be lowest in September compared to June and July and higher at mid-day than in the evenings and nights (Gunnlaugsdottir 2022). Moisture availability plays an important role in the metabolic activity of microbes and enzymes as the activity is inhibited when moisture is limited or in excess (Sheik et al. 2011; Allison & Treseder 2008). In the current study, where soil moisture content was 54% during the wet conditions, soil respiration was suppressed.

This study has demonstrated the response of biocrust from the highlands of Iceland to experimental warming under varying moisture conditions. Warming had a negative effect on biocrust respiration rate only under the dry moisture condition. The outcome of the study provides grounds for further studies on subarctic ecosystems dominated by biocrust. At the CRUST site, warming has been found to increase ecosystem functions, such as N fixation rates, especially when moisture was at a saturation level and only when light was not limited (Salazar et al. 2022). To fully explore how warming impacts biocrust respiration in the high north, future studies might consider mesic soil moisture that falls between the dry and wet moisture regimes. Moreover, CO_2 flux studies at the CRUST site should be continued in order to determine the effect of experimental warming on subarctic biocrust CO_2 modulations over a longer period of time.

5. CONCLUSIONS

This study provides some insight into the respiratory responses of subarctic biocrust to experimental warming under different moisture conditions. The study aimed at assessing the effect of warming on inter-annual respiration rates and establishing the relationship between soil moisture and temperature to soil respiration. The data used for the study on soil temperature, moisture and respiration were collected during the month of June in 2019 and 2022.

The results suggest that there was no effect of warming on soil moisture under both dry and wet conditions. However, the effect of warming on soil temperature was positive only under dry conditions. Moreover, warming had a negative effect on biocrust respiration rate only under dry conditions. Under wet conditions, there was no effect of warming on soil respiration rate.

The results further suggest that respiration rate was negatively correlated to soil moisture and positively correlated to soil temperature within the temperature and moisture ranges analysed. A better understanding of these relationships, however, requires more thorough analyses of temperature and soil water content limitation to soil respiration under a wider range of moisture regimes, including mesic.

ACKNOWLEDGEMENTS

I take this opportunity to express my gratitude to the GRÓ Land Restorative Training (GRÓ LRT) Programme for the opportunity to undertake the six-month training on land restoration. My heartfelt appreciation goes to the GRÓ LRT staff, particularly Sjöfn Vilhelmsdóttir, Berglind Orradottir, Brita Berglund and Halldora Traustadottir, as well as the lecturers from the Agricultural University of Iceland, University of Iceland and the Soil Conservation Service of Iceland for their immense support, guidance and encouragement throughout the programme. My sincere thanks also go to my supervisor, Dr Alejandro Villegas Salazar, for his expert guidance, advice and support through all the stages of this project work which improved the quality and standard of the project report. I wish to also thank the CRUST team members, particularly Ólafur Sigma Andrésson and Ian Klupar, for their contribution and support in gathering the data for this study. My final gratitude goes to the Director of the CSIR-Soil Research Institute for granting me the opportunity to attend this training program.

LITERATURE CITED

Allison SD, Treseder KK (2008) Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. Global Change Biology 14:2898-2909

Bates D, Machler M, Bolker B, Walker S (2015) Fitting linear mixed-effect models using lme4. Journal of Statistical Software 67:1-48.

Belnap J, Weber B, Büdel B. 2016. Biological soil crusts as an organizing principle in drylands. Springer International, Basel

Berdugo M, Delgado-Baquerizo M, Soliveres S, Hernández-Clemente R, Zhao Y, Gaitán JJ, et al. (2020) Global ecosystem thresholds driven by aridity. Science 367:787-790

Bond-Lamberty B, Thomson A (2010) Temperature-associated increases in the global soil respiration record. Nature 464:579-582

Borchhardt N, Schiefelbein U, Abarca N, Boy J, Mikhailyuk T, Sipman HJM, et al. (2017) Diversity of algae and lichens in biological soil crusts of Ardley and King George islands, Antarctica. Antarctic Science 29:229-237

Bowker MA, Belnap J, Büdel B, et al. 2016. Controls on distribution patterns of biological soil crusts at micro- to global scales. In: Weber B, Büdel B, and Belnap J (Eds). Biological soil crusts: an organizing principle in drylands. Springer, Berlin

Castillo-Monroy AP, Maestre FT, Rey A, Soliveres S, García-Palacios P (2011) Biological soil crust microsites are the main contributor to soil respiration in a semiarid ecosystem. Ecosystems 14:835-847

Cheng C, Gao M, Zhang Y, Long M, Wu Y, Li X (2021) Effects of disturbance to moss biocrusts on soil nutrients, enzyme activities, and microbial communities in degraded karst landscapes in southwest China. Soil Biology and Biochemistry 152:108065

Coe KK, Belnap J, Sparks JP (2012) Precipitation-driven carbon balance controls survivorship of desert biocrust mosses. Ecology 93:1626-1636

Darrouzet-Nardi A, Reed SC, Grote EE, Belnap J (2015) Observations of net soil exchange of CO_2 in a dryland show experimental warming increases carbon losses in biocrust soils. Biogeochemistry 126:363-378

Darrouzet-Nardi A, Reed SC, Grote EE, Belnap J (2018) Patterns of longer-term climate change effects on CO2 efflux from biocrusted soils differ from those observed in the short term. Biogeosciences 15:4561-4573

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165-173

Delgado-Baquerizo M, Gallardo A, Covelo F, Prado-Comesaña A, Ochoa V, Maestre FT (2015) Differences in thallus chemistry are related to species-specific effects of biocrust-forming lichens on soil nutrients and microbial communities. Functional Ecology 29:1087-1098

Dias T, Crous CJ, Ochoa-Hueso R, Manrique E, Martins-Loução MA, Cruz C (2020) Nitrogen inputs may improve soil biocrusts multifunctionality in dryland ecosystems. Soil Biology and Biochemistry 149:107947

Duran P, Mora M de la L, Matus F, Barra PJ, Jofré I, Kuzyakov Y, et al. (2021) Biologicalcrusts to increase soil carbon sequestration: new challenges in a new environment. Biology 10:1-13

Elbert W, Weber B, Burrows S, Steinkamp J, Büdel B, Andreae MO, et al. (2012) Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. Nature Geoscience 5:459-462

Escolar C, Maestre FT, Rey A (2015) Biocrusts modulate warming and rainfall exclusion effects on soil respiration in a semi-arid grassland. Soil Biology and Biochemistry 80:9-17

Fang C, Ye JS, Gong Y, Pei J, Yuan Z, Xie C, et al. (2017) Seasonal responses of soil respiration to warming and nitrogen addition in a semi-arid alfalfa-pasture of the Loess Plateau, China. Science of the Total Environment 590-591:729-738

Fang C, Li F, Pei J, Ren J, Gong Y, Yuan Z, et al. (2018) Impacts of warming and nitrogen addition on soil autotrophic and heterotrophic respiration in a semi-arid environment. Agricultural and Forest Meteorology 248:449-457

Fischer T, Veste M, Wiehe W, Lange P (2010) Water repellency and pore clogging at early successional stages of microbiotic crusts on inland dunes, Brandenburg, NE Germany. Catena 80:47-52

Guan C, Zhang P, Zhao C, Li X (2021) Effects of warming and rainfall pulses on soil respiration in a biological soil crust-dominated desert ecosystem. Geoderma 381:114683

Gunnlaugsdottir GE (2022) Experimental warming of subarctic biocrust : temporal responses of soil respiration and plant community. Master’s thesis, University of Helsinki and Agricultural University of Iceland.

Henry GHR, Molau U (1997) Tundra plants and climate change: The international tundra experiment (ITEX). Global Change Biology 3:1-9

Intergovernmental Panel on Climate Change (IPCC) (2022) Climate change 2022: mitigation of climate change - summary for policymakers (SPM). Cambridge University Press:1-30

Jia R, Chen N, Yu K, Zhao C (2019) High rainfall frequency promotes the dominance of biocrust under low annual rainfall. Plant and Soil 435:257-275

Jones CG, Lawron JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946-1957

Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and Biochemistry 27:753-760

Li J, Wang G, Mayes MA, Allison SD, Frey SD, Shi Z, et al. (2019) Reduced carbon use efficiency and increased microbial turnover with soil warming. Global Change Biology 25:900-910

Maestre FT, Escolar C, de Guevara ML, Quero JL, Lázaro R, Delgado-Baquerizo M, et al. (2013) Changes in biocrust cover drive carbon cycle responses to climate change in drylands. Global Change Biology 19:3835-3847

Manzoni S, Schaeffer SM, Katul G, Porporato A, Schimel JP (2014) A theoretical analysis of microbial eco-physiological and diffusion limitations to carbon cycling in drying soils. Soil Biology and Biochemistry 73:69-83

Marion GM, Henry GHR, Freckman DW, Johnstone J, Jones G, Jones MH, et al. (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology 3:20-32

Moreno-Jiménez E, Ochoa-Hueso R, Plaza C, Aceña-Heras S, Flagmeier M, Elouali FZ, et al. (2020) Biocrusts buffer against the accumulation of soil metallic nutrients induced by warming and rainfall reduction. Communications Biology 3:1-8

Moyano FE, Manzoni S, Chenu C (2013) Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. Soil Biology and Biochemistry 59:72-85

Nevins CJ, Strauss SL, Inglett PW (2020) Biological soil crusts enhance moisture and nutrients in the upper rooting zone of sandy soil agroecosystems. Journal of Plant Nutrition and Soil Science 183:615-626

Peng F, Manhou X, Quangang Y, Xuhui Z, Tao W, Xian X (2015) Different responses of soil respiration and its components to experimental warming with contrasting soil water content. Arctic, Antarctic, and Alpine Research 47:359-368

Pietrasiak N, Regus JU, Johansen JR, Lam D, Sachs JL, Santiago LS (2013) Biological soil crust community types differ in key ecological functions. Soil Biology and Biochemistry 65:168-171

Pointing SB, Belnap J (2012) Microbial colonization and controls in dryland systems. Nature Reviews Microbiology 10:551-562

Porada P, Weber B, Elbert W, Pöschl U, Kleidon A (2013) Estimating global carbon uptake by lichens and bryophytes with a process-based model. Biogeosciences 10:6989-7033

Quan Q, Tian D, Luo Y, Zhang F, Crowther TW, Zhu K, et al. (2019) Water scaling of ecosystem carbon cycle feedback to climate warming. Science Advances 5:1-8

R-Core-Team. (2020). R: a language and environment for statistical computing.

Rodriguez-Caballero E, Belnap J, Büdel B, Crutzen PJ, Andreae MO, Pöschl U, et al. (2018) Dryland photoautotrophic soil surface communities endangered by global change. Nature Geoscience 11:185-189

Rousk K, Degboe J, Michelsen A, Bradley R, Bellenger JP (2017) Molybdenum and phosphorus limitation of moss-associated nitrogen fixation in boreal ecosystems. New Phytologist 214:97-107

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, et al. (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543-562

Salazar A, Rousk K, Jónsdóttir IS, Bellenger JP, Andrésson ÓS (2020) Faster nitrogen cycling and more fungal and root biomass in cold ecosystems under experimental warming: a meta-analysis. Ecology 101:1-13

Salazar, A., Warshan, D., Vasquez-Mejia, C., & Andrésson, Ó. S. (2022). Environmental change alters nitrogen fixation rates and microbial parameters in a subarctic biological soil crust. bioRxiv. https://doi.org/10.1101/2022.01.25.477655

Sancho LG, Belnap J, Colesie C, et al (2016) Carbon Budgets of Biological Soil Crusts at Micro-, Meso-, and Global Scales. Pages 287-304. In: Weber B, Büdel B, Belnap J (eds) Biological soil crusts: an organizing principle in drylands. Springer International, Cham

Schindlbacher A, Wunderlich S, Borken W, Kitzler B, Zechmeister-Boltenstern S, Jandl R (2012) Soil respiration under climate change: prolonged summer drought offsets soil warming effects. Global Change Biology 18:2270-2279

Sheik CS, Beasley WH, Elshahed MS, Zhou X, Luo Y, Krumholz LR (2011) Effect of warming and drought on grassland microbial communities. ISME Journal 5:1692-1700

Sinsabaugh RL, Manzoni S, Moorhead DL, Richter A (2013) Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. Ecology Letters 16:930-939

Stewart KJ, Coxson D, Grogan P (2011) Nitrogen inputs by associative cyanobacteria across a low arctic tundra landscape. Arctic, Antarctic, and Alpine Research 43:267-278

Tóth M, Fekete I, Barta K, Farsang A (2020) Measurement of soil CO_2 respiration on arable land treated by sewage sludge compost. Geosciences and Engineering 8:305-311

Tucker CL, Ferrenberg S, Reed SC (2019) Climatic sensitivity of dryland soil CO^2 fluxes differs dramatically with biological soil crust successional state. Ecosystems 22:15-32

Unger IM, Kennedy AC, Muzika RM (2009) Flooding effects on soil microbial communities. Applied Soil Ecology 42:1-8

USDA (2014) Soil: an essential link in the cycle of life. Advances:1-8

Warren SD (2001) Synopsis: influence of biological soil crusts on arid land hydrology and soil stability. 150:349-360

Weber B, Belnap J, Büdel B, Antoninka AJ, Barger NN, Chaudhary VB, et al. (2022) What is a biocrust? A refined, contemporary definition for a broadening research community. Biological Reviews

Williams L, Loewen-Schneider K, Maier S, Büdel B (2016) Cyanobacterial diversity of western European biological soil crusts along a latitudinal gradient. FEMS Microbiology Ecology 92:1-9

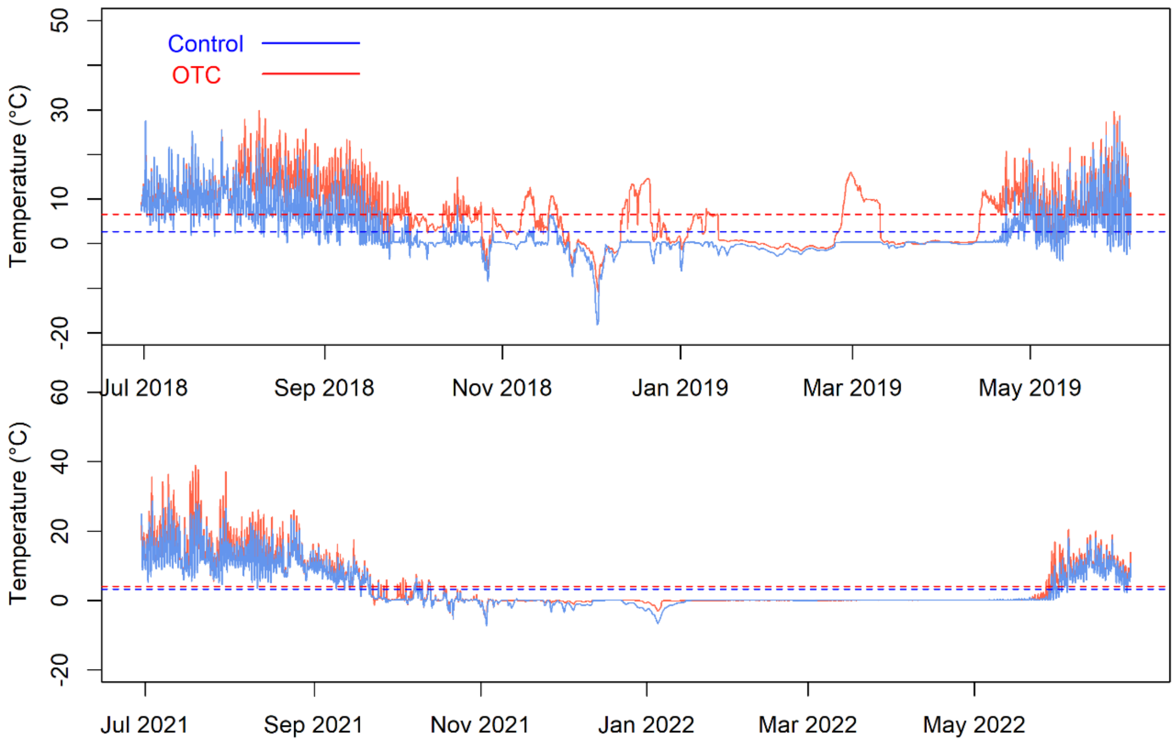
Zelikova TJ, Housman DC, Grote EE, Neher DA, Belnap J (2012) Warming and increased precipitation frequency on the Colorado Plateau: implications for biological soil crusts and soil processes. Plant and Soil 355:265-282

Zhang B, Zhang Y, Su Y, Wang J, Zhang J (2013) Responses of microalgal-microbial biomass and enzyme activities of biological soil crusts to moisture and inoculated microcoleus vaginatus gradients. Arid Land Research and Management 27:216-230

Zhang Y, Guo S, Liu Q, Jiang J, Wang R, Li N (2015) Responses of soil respiration to land use conversions in degraded ecosystem of the semi-arid Loess Plateau. Ecological Engineering 74:196-205

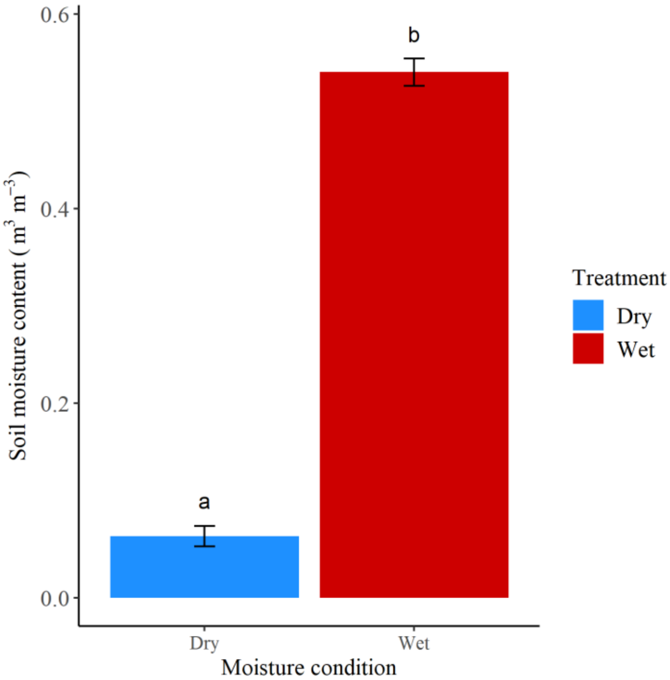
APPENDICES

Appendix I



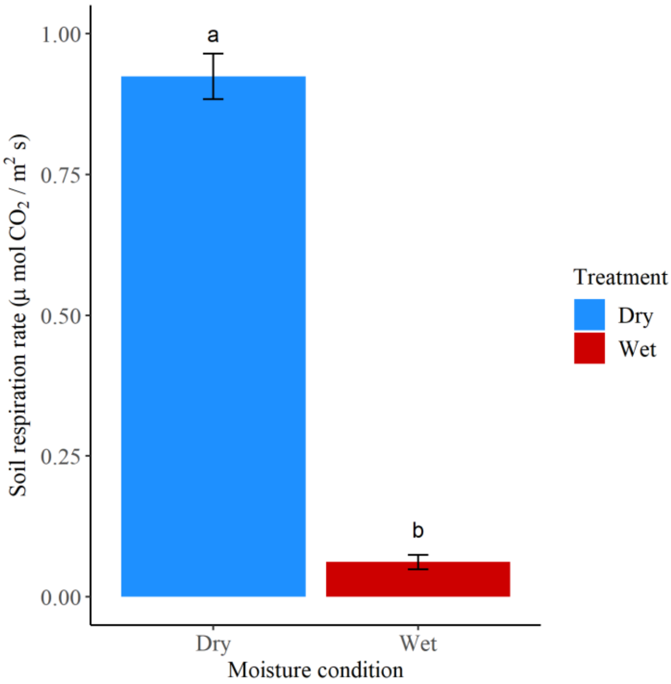
Yearly soil temperature from top) July 2018 to June 2019, and bottom) July 2021 to June 2022 in the OTC and control plots.

Appendix II



Soil moisture content under different moisture conditions of Dry (June 2019) and Wet conditions (June 2022).

Appendix III



Soil respiration rate under different moisture conditions of Dry (June 2019) and Wet (June 2022).