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Impact of warming on *Nostoc* colonies (Cyanobacteria) in a wet hummock meadow, Spitsbergen

Josef ELSTER[1,2*], Jana KVÍDEROVÁ[1,2*], Tomáš HÁJEK[1,2], Kamil LÁSKA[1,3] and Miloslav ŠIMEK[1,4]

[1] *University of South Bohemia, Faculty of Science, Branišovská 31, 370 05 České Budějovice, Czech Republic*

[2] *Institue of Botany AS CR, Dukelská 135, 379 82 Třeboň, Czech Republic*

[3] *Masaryk University, Faculty of Science, Kotlářská 2, 611 37 Brno, Czech Republic*

[4] *Institute of Soil Biology, Biology Centre AS CR, Na Sádkách 7, 370 05 České Budějovice, Czech Republic*

[*] *<jelster@butbn.cas.cz> <kviderova@butbn.cas.cz>*

Abstract: In order to simulate the warming effects on Arctic wetlands, three passive open-top chambers (OTCs) and three control cage-like structures (CCSs) equipped with soil temperature and soil volumetric water content (VWC) probes for continuous microclimatic measurements were installed in a wet hummock meadow, Petuniabukta, Billefjorden, central Spitsbergen, in 2009. The warming effects on primary productivity were investigated during summer seasons 2009 and 2010 in cyanobacterial colonies of *Nostoc commune* s.l., which plays an important role in the local carbon and nitrogen cycles. The microclimatic data indicated that the effect of OTCs was dependent on microtopography. During winter, two short-term snow-thaw episodes occurred, so that liquid water was available for the *Nostoc* communities. Because of the warming, the OTC hummock bases remained unfrozen three weeks longer in comparison to the CCSs and, in spring, the OTC hummock tops and bases exceeded 0°C several days earlier than CCS ones. Mean summer temperature differences were 1.6°C in OTC and CCS hummock tops, and 0.3°C in the OTC and CCS hummock bases. The hummock tops were drier than their bases; however the VWC difference between the OTCs and CCSs was small. Due to the only minor differences in the microclimate of OTC and CCS hummock bases, where the *Nostoc* colonies were located, no differences in ecophysiological characteristics of *Nostoc* colonies expressed as photochemistry parameters and nitrogenase activities were detected after two years exposition. Long-term monitoring of *Nostoc* ecophysiology in a manipulated environment is necessary for understanding their development under climate warming.

Key words: Arctic, Svalbard, Cyanobacteria, nitrogenase activity, photosynthesis.

Introduction

In Arctic hydro-terrestrial environments, considerable, *i.e.* visible, amounts of microalgal and cyanobacterial biomass can accumulate over a long time period

(Vincent 2000; Elster 2002). Cyanobacteria play a dual role there. Besides being considerable primary producers, they are able to fix atmospheric nitrogen, thus being an important source of nitrogen for other organisms. Nitrogen often limits primary production in the Arctic (Henry and Svoboda 1986; Davey and Rothery 1992; Liengen and Olsen 1997; Walker *et al.* 2008; etc.).

The climate change significantly influences current temperature and moisture conditions in Arctic ecosystems. The predicted effects of a doubling of the atmospheric CO_2 will be dramatic; mean annual temperatures in the Arctic may be 3–5°C higher within 100 years (Maxwell 1992; ACIA 2004; Callaghan *et al.* 2004a; Callaghan *et al.* 2004b). Most models also predict that the overall annual global precipitation will increase. Temperature and precipitation increases will have a large impact on cyanobacteria and microalgae community structure, and also on their *in situ* ecophysiological performance (photochemical processes and nitrogen fixation; Elster *et al.* 2001; Callaghan *et al.* 2004a, b), as water and temperature are the major environmental predictors of species survival in the Arctic. Even slight increases in temperature and precipitation could lead to a development of a deeper active layer, higher rates of chemical transformation and, ultimately, greater nutrient availability (Shaver *et al.* 2000; Rolph 2003; Walker *et al.* 2008).

It remains unclear how climate warming will affect nitrogen fixation. Some authors predict, that future Arctic environments will experience increased nitrogen fixation due to heightened enzymatic activity and increased concentration of carbon dioxide, while others predict that nitrogen fixation will be inhibited by increased available nitrogen due to increased mineralization acting as a negative feedback upon this process (Paul and Clark 1996; Walker *et al.* 2008).

Many field studies have been conducted on the potential effects of global warming on the growth and community structure of vegetation, soil bacterial and invertebrate community performances in various polar/alpine ecosystems (Marion *et al.* 1997; Hollister and Webber 2000; Walker *et al.* 2008; Rinnan *et al.* 2009b). By contrast, equivalent experimental studies on cryptogams (mosses, lichens, cyanobacteria and microalgae) in the Arctic are much sparser and comparative studies across sites are missing. Since cryptogams are the main primary producers in high Arctic wetlands, any change in their growth or community structure caused by climate change will affect the local ecosystem.

Passive open-top chambers (OTC) are the most frequent manipulation technique in these *in situ* warming experiments (Chapin and Shaver 1985; Strathdee and Bale 1993; Kennedy 1995; Marion *et al.* 1997; Day *et al.* 1999; Hollister and Webber 2000; Convey *et al.* 2002). This technique is standardized in design and forms part of a broader geographical network of sites (e.g. The International Tundra Experiment, ITEX), which allows for a comparison of responses on a circumpolar scale (Molau and Mølgaard 1996).

Our experimental locality in Petuniabukta, Billefjorden, Central Svalbard, the Norwegian Arctic, is situated in a wet hummock meadow. The meadow is satu-

rated with water at the beginning of the vegetation season due to extensive snowfield melting, however it gradually dries during summer and early fall (Kvíderová *et al.* 2011). The desiccation process can be interrupted by short rain events that could supply the tundra with water again. Tundra vegetation can be subjected to repeated cycles of drying and re-hydration. In this hydro-terrestrial ecosystem, the *N. commune* colonies are the most significant nitrogen source (Liengen and Olsen 1997; Vincent 2000; Kvíderová *et al.* 2011). These colonies are very abundant and produce high biomass, which significantly contributes to the local carbon and nitrogen cycles (Kvíderová *et al.* 2011).

In this paper, we report on the first two years (2009 and 2010) of *in situ* experiments, using passive open-top chambers to simulate warming, and control treatments in a wet hummock meadow, Petuniabukta, Billefjorden, Central Svalbard. The tasks of this field experiments are:

- To describe the microclimatic environment (surface soil layer temperature and volumetric water content in the vegetative seasons, non-vegetative seasons and transition period) including water chemistry of the wet hummock meadow under natural (control) and *in situ* warming simulation.
- To compare the microclimatic parameters (temperature and volumetric water content in hummock tops and bases) in the OTCs and control treatments in order to estimate the OTC efficiency of warming.
- To evaluate photochemical performance and nitrogenase activity (nitrogen fixation) of *N. commune* colonies in the wet hummock tundra in manipulated and non-manipulated environments.
- To relate the microclimatic data with physiological performance of *N. commune* in the wet hummock tundra in manipulated and non-manipulated environments.

Methods

Site description and experimental design

The experimental site is located in a wet hummock meadow at Petuniabukta, Billefjorden, Central Svalbard (N 78°43’49” E 16°26’41”, 15 m a.s.l.) where the vegetation is dominated by mosses (see vegetation type unit “Vegetation dominated by mosses” description in Prach et al., this issue). Hummocks are 15–20 cm high, about 20–30 cm in diameter and there are about 2–3 hummocks per 1m^2. In summer 2009, three Open-top Chambers (OTC) and three Control Cage-like Structures (CCSs) were installed at the experimental locality (Fig. 1A). The OTC was designed as a hexagonal chamber with a bottom diameter of 140 cm (side length of 70 cm), top diameter of 90 cm (side length of 45 cm), and height of 50 cm. The area of each OTC was 1.27 m^2. The chambers had inwardly inclined sides (60° with respect to horizontal), which improved transmittance of solar radiation and helped to trap heat. The chambers were constructed of Perspex (Quinn XT FL

5 mm thick, Quinn Plastics, Ireland) designed specifically for solar applications. This material had high solar transmittance in the visible wavelengths (90%) and low transmittance in the infrared (heat) range (<5%). The tops of OTCs were covered by fencing over winter. The control treatments CCSs were designed as a cage of equal length and width of 90 cm, and height of 40 cm. The area of each CCS was 0.81 m^2. The cages were welded together with a 0.8 cm diameter iron pole stand and covered by a wire screen. The entire experimental area is surrounded by a wooden ring fence. The screen of the CCS and tops of the OTCs protected these structures against damages e.g. from the Arctic fox, while the wooden ring fence prevented a reindeer grazing. Construction of the OTC device is described in more detail in the ITEX manual (Molau and Mølgaard 1996).

Water level and water physico-chemical parameters

In addition to the manipulation experiment, water level and water physico-chemical parameters in the wet hummock meadow were monitored. A transect of 4 parallel rows of holes 30 cm deep were drilled into the permafrost across the experimental plots. A polyethylene tube, 5cm diameter, with a densely perforated wall, was installed inside each hole (Fig. 1B), in which the water level was measured by a builder's tape. Simultaneously, water from the tubes was sucked up by a syrette with tubes, filtered through a pre-rinsed Whatman filter paper GF/C in the field and transferred to two acid-washed polythene bottles (100 ml). The first bottle was frozen for transport to the Czech Republic, while the second was used in situ for measurements of pH and conductivity (Kombibox WTE, Weilheim, CB 570).

Inorganic nitrogen and phosphorus concentrations were determined using a Flow Injection Analyser (FIA, Tecator, Sweden; Růžička and Hansen 1981). Dissolved reactive phosphorus (DRP; PO_4-P) was analysed by reaction with ammonium molybdate and reduction by stannous chloride to phosphomolybdenum blue (Proctor and Hood 1954, Application note AN60-83 Tecator). The detection limit for DRP was 5 µg l^{-1}. Nitrate- (NO_3-N) and nitrite- (NO_2-N) nitrogen were analysed by reaction with sulphonamide (Application note ASN 62-01-83) and ammonium-nitrogen (NH_4-N) by the gas diffusion method (Karlberg and Twengstrom 1983, Application note ASN 50-0187 Tecator). The detection limit for NH_4-N was 10 and for NO_3-N was 3 µg l^{-1}. For total nitrogen (TN) and total phosphrus (TP) determination, the samples were treated by persulfate mineralization at 151°C for 30 min. The concentration of Cl ions was determined by reaction with mercury thiocyanate and ferric ions (Růžička *et al.* 1976, Application note AN 63/83 Tecator, detection limit 5 µg l^{-1}). The SO_4-S content was analyzed by FIA (Madsen and Murphy 1981, Application note ASTN42/86 Tecator, detection limit 10 µg l^{-1}). The dissolved substances (dry weight, DW) content was determined by evaporation and drying at 105°C (Howard 1933; Sokoloff 1933). Cation contents (Na, K, Ca, Mg) were analyzed by a Varian Spectra AA 640 polarized atomic absorption spectrophotometer (Techtron, Australia). A 300 mg sample was

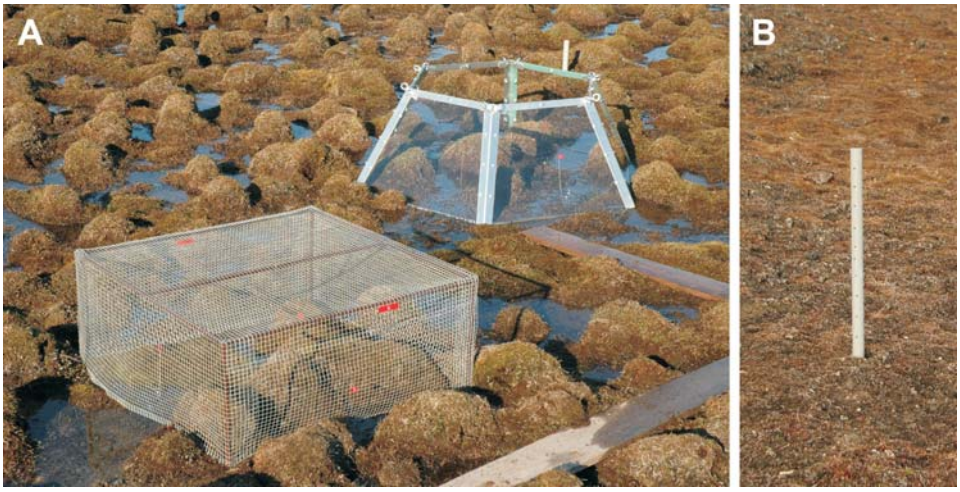

Fig. 1. The experimental site in the wet hummock meadow in Petuniabukta. **A**. Control cage-like structure (left) and passive open-top chamber (right). **B**. Tube for water sampling. The distance between the holes is 5 cm.

weighed into a thick-wall test tube and concentrated HNO_3 of volume 0.75 ml and concentrated HCl of volume 2.2 ml were added. The tube was closed with a loose stopper. The sample was mixed and let to stand at ambient temperature for 16 hrs. After that time, the sample was boiled at 120°C for 2 hrs. Then the sample was cooled and filtered quantitatively into a 50ml volumetric flask. The 5% HNO_3 was added to get the final sample volume of 50 ml. For determination of cations concentration by atomic absorption spectrophotometry, the acetylele-air flame analysis method was used for Na, K and Mg, and N_2O-acetylene flame analysis of Ca.

Microclimatic parameters

In each treatment soil temperature and volumetric water content (VWC) were permanently monitored approximately in the central part of each OTC and/or CCS at the bases and tops of the hummocks. The soil capacitance method was used to measure volumetric water content at a depth of ~2 cm below the ground. In total, ten ECH_2O EC-5 soil moisture probes (Decagon Device Inc., USA) and ten Pt100/8 thermometers (EMS, Czech Republic) were inserted completely into the substrate within the OTCs and CCSs. The ECH2O EC-5 probe dimensions were 5 × 2 × 0.1 cm which allowed for measurement of the apparent dielectric constant of soil within a 2 cm zone on both flat sides of the probe. An EdgeBox V12 multichannel datalogger (EMS, Czech Republic) was used to excite and measure the output from the ECH2O EC-5 soil moisture probes. The datalogger supplied 2.5V to each ECH2O EC-5 probes and the outputs were converted by the calibration equation for mineral soils (Parsons and Bandaranayake 2009). The output from all probes was measured and stored at 60 min intervals.

Fig. 2. Two types of exposition of *Nostoc commune* s.l. **A**. Petri dish. **B**. Exposition chamber.

Ecophysiological parameters of *Nostoc commune*

In summer 2009 three plastic Petri dishes (9 cm diameter), each with one colony of *N. commune*, were installed to each OTC and CCS. A dense net of holes was prepared by boring across the bottom and lid of each Petri dish. Filter paper was inserted on to the bottom of each Petri dish (Fig. 2A). The closed Petri dishes were kept in contact with the wet tundra surface by needles. In both experimental seasons (2009 and 2010), Petri dishes with *N. commune* colonies were regularly collected, put into a cool box and transported to the field laboratory for measurements of photochemical processes and nitrogenase activity.

Special Exposition Chambers (EC) were prepared in summer 2010, because of an expected greenhouse effect in the closed Petri dishes. These ECs were made from perplex glass tubes with a diameter of 12.5 cm; the same material was used for OTC construction. The top and bottom of each tube were covered by plastic nets (square holes with length of 0.5 cm), which were fixed by narrow plastic rings (Fig. 2B). In each experimental treatment (OTC and CCS) three ECs, with one *N. commune* colony in each, were in free contact with the moss tundra surface. In 2010, the *N. commune* colonies enclosed in the ECs were regularly measured like the Petri dishes. After measurements, all Petri dishes and ECs were returned exactly to the same place.

Weight, photochemical processes and nitrogenase activity were evaluated in each colony. The colony was weighed on a digital scale (Denver Instruments, Germany). Photochemical processes were measured by a FluorCam 700MF fluorescence imaging camera (Photon Systems Instruments, Czech Republic) using the quenching protocol. The *Nostoc* colony was dark-adapted for 4 hours before the measurement. Red measurement pulses of less than 3 μmol m^{-2} s^{-1} and lasting 33.3 μs were applied to obtain minimum fluorescence in the dark (F_0). A saturation pulse of white light of 2100 μmol m^{-2} s^{-1} lasting 800 ms was used to determine maximum fluorescence in the dark (F_M). The maximum quantum yield (F_V/F_M) was measured 10 s after the start of the measurement in the dark adaptation state and was followed by 40 s of dark relaxation (refer to Kvíderová *et al.* 2011 for protocol details). The photochemical parameter, maximum quantum yield during dark

adaptation (F_V/F_M), was calculated using the FluorCam 7 software (Photon Systems Instruments, Czech Republic) as according to Roháček and Barták (1999) and Maxwell and Johnson (2000). The equation used and detailed equation parameter descriptions are summarized in Kvíderová *et al.* (2011).

Nitrogenase activity (NA) was measured by acetylene-ethylene reduction assay (Stewart *et al.* 1967) in 100 mL glass flasks after 90 min incubation. Ethylene in the samples was quantified with a gas chromatograph and nitrogenase activity was expressed in nmol/h C_2H_4 per g fresh biomass. The details of the nitrogenase activity evaluation are given in Kvíderová *et al.* (2011).

Statistical evaluation

All statistical evaluations were performed using Statistica 9.0 (StatSoft, USA); differences were considered significant at $P < 0.05$ (probability of Type I Error: null hypothesis is rejected when it is true). All data were tested for normality before the statistical evaluation. The non-parametric Kruskal-Wallis test was used for evaluation of differences in physico-chemical parameters at the site below the terrace and the experimental site (n = 10 in each sampling). The homologous groups determined by the ANOVA/HSD test for unequal n at a significance level of 0.05 were used for evaluating the differences in temperature and soil water content at the bases and tops of each OTC and CCS for the whole experiment and vegetative season only (n = 3 for OTC and n = 2 for CCS in each data record; total of n = 13210 for all temperature data from one probe and n = 10199 for all VWC data from one probe were used for key data determination). Paired t-test was used to evaluate the inter-seasonal difference in number of "drought" days as an indicator of the difference in water availability at the experimental locality (n = 10 for each year). The homologous groups determined by the ANOVA/Tukey HSD test at a significance level of 0.05 were used for evaluating warming effects on *Nostoc* colonies (n = 9 in each treatment). Correlation analysis was performed to evaluate the relationship between instantaneous microclimate conditions (temperature, VWC) and ecophysiological parameters (weight, F_V/F_M and nitrogenase activity) of the *Nostoc* colonies (Petri dishes: n = 36 for temperature and n = 63 for VWC in OTCs, n = 24 for temperature and n = 42 for VWC in CCSs; ECs: n = 27 in OTC and n = 18 in CCS for both variables), and the relationship between water level depth and *Nostoc* colonies ecophysiology (Petri dishes: n = 63 in OTC, n = 42 in CCS; ECs: n = 27 in OTC, n = 18 in CCS).

Results

Water level and water physico-chemical parameters

Water levels in the wet hummock meadow greatly differed in the 2009 and 2010 summer seasons (Fig. 3). In 2009, the water level was well balanced through the whole season, while in 2010 the water level decreased in the first half of the season

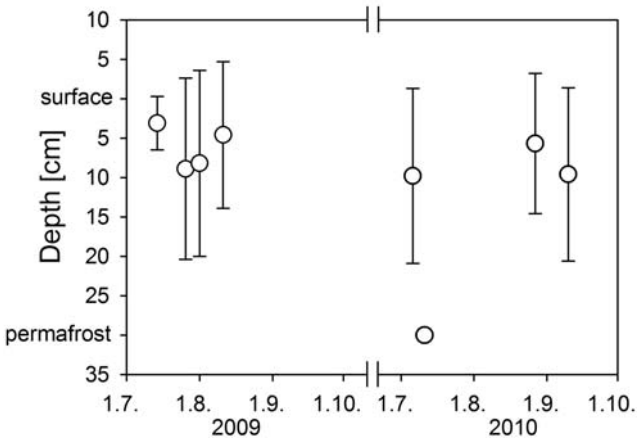

Fig. 3. Water levels at the experimental locality (mean ± standard deviation, n = 10 in each sampling date) in both the 2009 and 2010 growing seasons.

due to the much smaller snow field in the upper part of the wet meadow, but came back during the second half of the season. However, the ranges of the standard deviation bars indicated that water level in all 9 measuring points differed due to microhabitat diversity. In particular, microhabitat water level can be several centimetres below the surface, while a shallow surface pool could occur just a few meters away.

Water physico-chemical parameters are given in Table 1. Because of the drier second season (see below), the TP and DW values were slightly higher in 2010 than in 2009. On the contrary, NH_4-N was slightly higher in 2009. In 2009, the reduced form of ammonium-nitrogen in the wet environment could not be oxidised into nitrate and nitrite forms. In 2009 at the upper part of the experimental site, below the terrace from where water was flowing into the meadow, NO_2-N, NO_3-N, TN, PO_4-P and TP concentrations were higher than in the meadow, since most of the mineral nutrients were in the inflowing water. The decrease of pH in the experimental field could be caused by calcium, magnesium and sulphate precipitation. In the drier 2010 season, the physical and chemical parameters of samples from below the terrace and the experimental field were comparable with the exception of lower NO_3-N at the OTC area. Such a decrease was observed also in 2009. This could indicate nitrate consumption by the meadow vegetation.

Microclimatic parameters

Temperature. — The microclimate monitoring was initiated at the hummock wet meadow in July 2009 and continued through the winter season till September 2010. However, soil temperature data acquired from July to December 2009 were not included in the analysis and subsequent evaluation due to bad quality and the occurrence of missing values in the data set. The courses of soil temperature at the

Table 1

The physico-chemical parameters (mean ± standard deviation) of the site below the terrace and the experimental field during the 2009 and 2010 seasons; n – number of samples, statistical significance (non-parametric Kruskal-Wallis test) * – P <0.05, ** – P <0.01, *** – P <0.001.

		2009			2010		
		all samples	below terrace	experimental field	all samples	below terrace	experimental field
		n = 23	n = 19	n = 4	n = 24	n = 5	n = 21
pH		7.61 ± 0.45	8.30 ± 0.44	7.47 ± 0.36**	7.52 ± 0.23	7.77 ± 0.04	7.48 ± 0.25
Conductivity	µS cm^{-1}	689 ± 223	831 ± 656	666 ± 95	814 ± 217	626 ± 73	841 ± 218
NH_4-N	µg l^{-1}	140 ± 77	249 ± 126	121 ± 56	55.0 ± 53.5*	67.4 ± 16.5	53.2 ± 56.9
NO_2-N	µg l^{-1}	4.09 ± 7.92	15.1 ± 21.8	2.24 ± 0.47*	3.18 ± 1.41***	3.49 ± 0.50	3.13 ± 1.50
NO_3-N	µg l^{-1}	82.3 ± 77.8	249 ± 82	49.9 ± 13.2**	133 ± 270	150 ± 66	131 ± 288*
TN	µg l^{-1}	539 ± 175	768 ± 206	491 ± 138*	620 ± 322	687 ± 85	611 ± 343
PO_4-P	µg l^{-1}	22.7 ± 16.0	52.4 ± 28.2	17.4 ± 5.0*	14.9 ± 13.9	18.4 ± 0.9	14.4 ± 14.9
TP	µg l^{-1}	42.5 ± 17.7	73.8 ± 37.8	37.5 ± 5.9*	58.2 ± 7.1***	62.1 ± 8.7	57.7 ± 6.9
Cl	mg l^{-1}	19.8 ± 58.6	99.5 ± 163.7	7.25 ± 2.32	11.5 ± 6.9**	10.7 ± 2.1	11.7 ± 7.3
DW	g l^{-1}	0.036 ± 0.024	0.021 ± 0.010	0.038 ± 0.026	0.065 ± 0.033*	0.050 ± 0.004	0.067 ± 0.035
Na	mg l^{-1}	15.0 ± 37.8	66.5 ± 105.4	6.90 ± 1.23	6.88 ± 3.16	5.69 ± 0.95	7.05 ± 3.33
K	mg l^{-1}	1.42 ± 2.23	4.41 ± 6.17	0.91 ± 0.17	1.46 ± 1.41	1.32 ± 0.38	1.48 ± 1.51
Ca	mg l^{-1}	134 ± 26	91.2 ± 11.7	141 ± 21	171 ± 55	126 ± 11.2	178 ± 56
Mg	mg l^{-1}	18.0 ± 4.0	19.8 ± 10.9	17.5 ± 2.3	21.0 ± 7.0	14.6 ± 3.9	21.9 ± 6.9
SO_4-S	mg l^{-1}	214 ± 107	205± 130	219 ± 109	246 ± 46	226 ± 27	249 ± 48

tops and bases of hummocks in the OTCs and CCSs were therefore processed from December 2009 till September 2010 (Fig. 4). Periods of temperature and volumetric water content (introduced later) measurements were divided into; (i) vegetative season 2009, (ii) non-vegetative season 2009-2010 including warming period in spring, (iii) transition period 2010, and (iv) vegetation season 2010 (Figs 4, 5 and Table 2). In both cases (OTC, CCS), temperatures fluctuated from 0°C down to -7 or -8°C from the start of measurements up to mid-June, 2010. There was a period with temperatures around 0°C resulting in a partial snow thawing in the second half of February 2010. During winter (non-vegetative season 2009/2010), the temperatures in both OTCs and CCSs were very similar, however, T_{max} was a little bit lower in the OTCs (about 0.2°C; Table 2). The surface of the soil in all experimental treatments warmed up to temperatures close to 0°C from the beginning of May (the non-vegetative season 2009/2010 – warming period in Table 2). The temperature reached -1°C in mid-May (transition period start date; Table 2) and, after this period, the temperature remained stable around 0°C (transition period in Table 2). The temperature of the OTC hummock tops reached positive values (vegetation season 2010) for several days earlier in comparison to the CCSs; a similar pattern was observed in the OTC and CCS hummock bases (Fig. 4). The duration of the transition period was the shortest in the OTC hummock tops, and the CCS hummock tops and bases, and was the longest in the OTC hummock bases (Table 2).

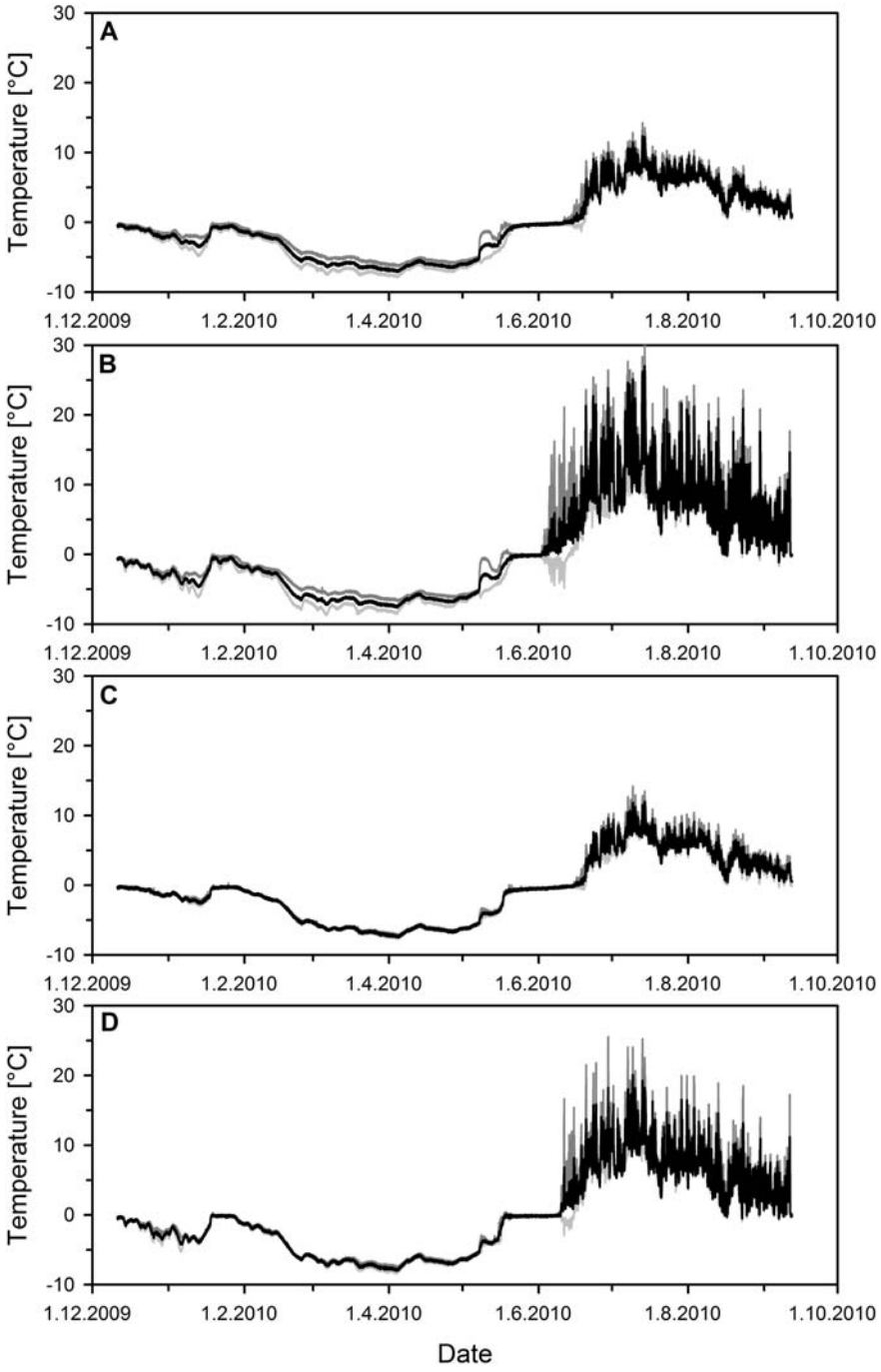

Fig. 4. Soil temperature in OTC and CCS hummock tops and bases during the experiment. **A**. OTC base. **B**. OTC top. **C**. CCS base. **D**. CCS top. Lines: black, mean (n = 3 for OTCs, n = 2 for CCSs); light gray, mean, standard deviation; dark gray, mean + standard deviation.

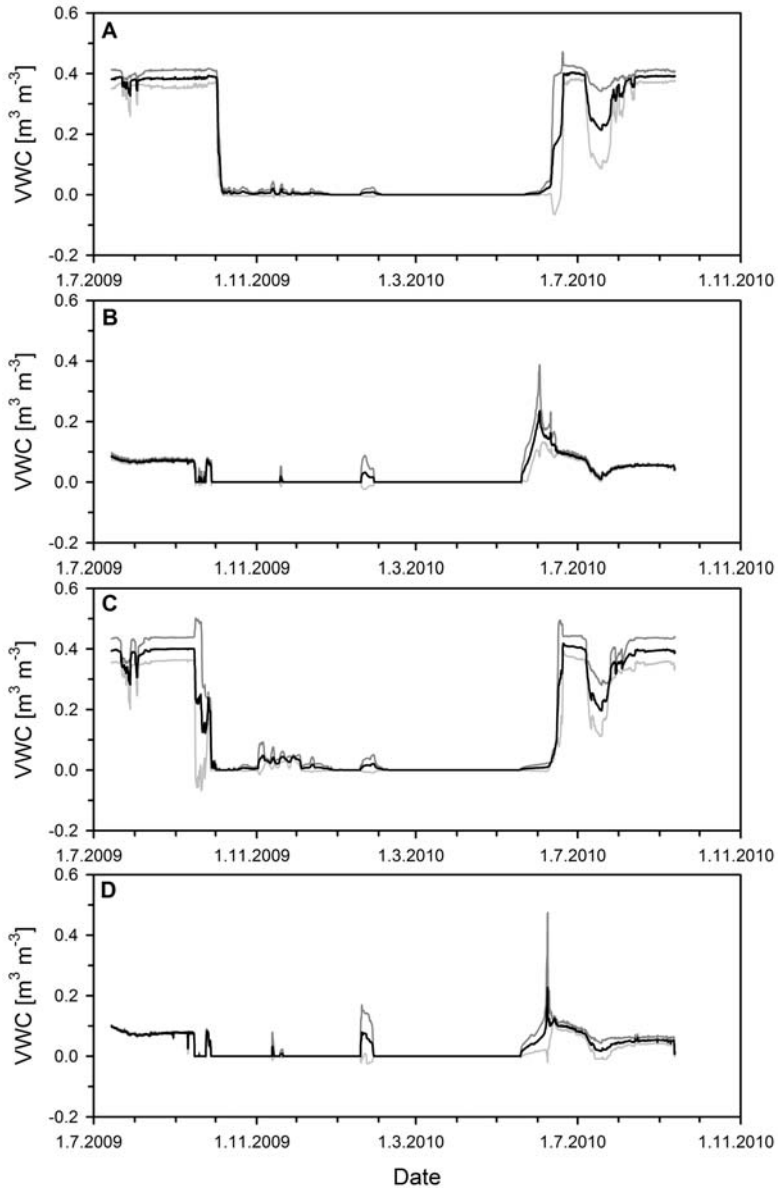

Fig. 5. Volumetric water content (VWC) in OTC and CCS hummock tops and bases during the experiment. **A**. OTC base. **B**. OTC top. **C**. CCS base. **D**. CCS top. Lines: black, mean (n = 3 for OTCs, n = 2 for CCSs), light gray, mean, standard deviation, dark gray, mean + standard deviation.

Above-zero temperatures were reached for the first time (0°C date; Table 2) in the OTC and CCS hummock tops as early as in mid- or late May 2010 (OTC hummock tops with the exception of OTC1 on 12.6.2010). Positive (above-zero) temperatures were reached in the OTC and CCS hummock bases almost one month later, in

Table 2

The seasonal characteristics (mean ± standard deviation; n = 13210 for all temperature data from one probe, n = 10199 for all VWC data from one probe) of the OTCs and CCSs. The letter indicates homologous groups as identified by an ANOVA/HSD test for unequal n at p = 0.05. Point definitions: Vegetative season end date = date on which the VWC dropped to 0 for the first time; $VWC_{refline}$ = steady-state VWC; drought = days when the VWC is lower than $VWC_{refline}$ – 10%; flood = days when the RWV is higher than $VWC_{refline}$ + 10%; non-vegetative season end date = date on which the temperature exceeded 0°C for the last time; warming period start date = date on which the temperature exceeded the warming threshold for the last time; warming threshold = non-vegetative T_{mn} – s.d.; warming period duration = number of days between the warming period start date and transition period start date; transition period start date = date on which the temperature exceeded -1.0°C for the first time; transition period duration = number of days between the transition period start date and vegetative season start date; 0°C date = date on which the temperature exceeded 0°C for the first time; wetting/thawing start date = date on which VWC exceeded 0 $m^3\ m^{-3}$ for the first time; wetting/thawing end date = date on which the VWC reached $VWC_{refline}$ for the first time; wetting/thawing period duration = number of days between wetting/thawing start date and wetting/thawing end date; vegetative period start = date on which the temperature remained above 0°C for whole day; vegetative period duration = number of days since the start of the vegetation period till 31.7.2010.

	OTC		CCS	
	top	base	top	base
Vegetative season 2009				
End date (VWC) [days]	15.9.2009 ± 1	2.11.2009 ± 48	15.9.2009 ± 0	30.9.2009 ± 1
VWC_{min} [$m^3\ m^{-3}$]	0.01 ± 0.01	0.00 ± 0.00	0.05 ± 0.07	0.00 ± 0.00
VWC_{mn} [$m^3\ m^{-3}$]	0.07 ± 0.01^a	0.31 ± 0.11^b	0.08 ± 0.00^a	0.34 ± 0.06^b
VWC_{max} [$m^3\ m^{-3}$]	0.09 ± 0.01^a	0.40 ± 0.03^b	0.10 ± 0.00^a	0.41 ± 0.04^b
$VWC_{refline}$ [$m^3\ m^{-3}$]	0.07 ± 0.01^a	0.38 ± 0.03^b	0.08 ± 0.01^s	0.40 ± 0.04^b
Drought [days]	5 ± 4	34 ± 46	1 ± 0	18 ± 1
Flood [days]	3 ± 4	0 ± 0	7 ± 2	0 ± 0
Non-vegetative season 2009/10				
End date [days]	27.5.2010 ± 15	9.6.2010 ± 4	18.5.2010 ± 1	13.6.2010 ± 3
T_{min} [°C]	-7.7 ± 1.0	-7.1 ± 0.8	-7.9 ± 0.6	-7.8 ± 0.1
T_{mn} [°C]	-4.2 ± 0.8	-3.5 ± 0.5	-3.9 ± 0.07	-3.8 ± 0.6
T_{max} [°C]	0.0 ± 0.0^a	0.0 ± 0.1^a	0.1 ± 0.1^{ab}	0.2 ± 0.01^b
Warming period start date [days]	29.4.2010 ± 4	3.5.2010 ± 4	1.5.2010 ± 4	1.5.2010 ± 5
Warming threshold	-6.5 ± 1.0	-5.9 ± 0.7	-6.5 ± 0.7	-6.3 ± 0.4
Warming period duration [days]	15 ± 3	12 ± 2	16 ± 4	16 ± 5
Transition period 2010				
Start [days]	15.5.2010 ± 6	15.5.2010 ± 6	16.5.2010 ± 1	17.5.2010 ± 0
Duration [days]	25 ± 1^a	32 ± 2^b	27 ± 4^{ab}	32 ± 2^{ab}
0°C date [days]	27.5.2010 ± 14	10.6.2010 ± 4	17.5.2010 ± 1	13.6.2010 ± 3
Wetting/thawing start date [days]	20.5.2010 ± 3	30.5.2010 ± 8	18.5.2010 ± 1	28.5.2010 ± 15
Wetting/thawing end date [days]	23.5.2010 ± 4^a	17.6.2010 ± 4^b	1.6.2010 ± 9^{ab}	18.6.2010 ± 1^b
Wetting/thawing period duration [days]	3 ± 1	18 ± 10	14 ± 8	21 ± 16

Table 2 – *continued*.

	OTC		CCS	
	top	base	top	base
Vegetative season 2010				
Start date (T) [days]	9.6.2010 ± 7	16.6.2010 ± 4	12.6.2010 ± 4	17.6.2010 ± 2
Vegetative season duration [days]	52 ± 7	45 ± 4	49 ± 4	44 ± 2
T_{min} [°C]	-1.3 ± 0.5^{a}	0.0 ± 0.1^{b}	-0.8 ± 0.1^{ab}	-0.2 ± 0.4^{b}
T_{mn} [°C]	8.4 ± 0.5^{a}	5.3 ± 0.2^{b}	6.8 ± 0.3^{c}	5.0 ± 0.1^{b}
T_{max} [°C]	28.2 ± 1.5^{a}	12.7 ± 1.5^{b}	20.6 ± 4.0^{c}	13.3 ± 0.4^{b}
VWC_{min} [m^3 m^{-3}]	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
VWC_{mn} [m^3 m^{-3}]	0.08 ± 0.01^{a}	0.30 ± 0.01^{b}	0.06 ± 0.02^{a}	0.31 ± 0.06^{b}
VWC_{max} [m^3 m^{-3}]	0.27 ± 0.12	0.41 ± 0.02	0.27 ± 0.19	0.42 ± 0.03
$VWC_{refline}$ [m^3 m^{-3}]	0.06 ± 0.00^{a}	0.39 ± 0.02^{b}	0.06 ± 0.01^{a}	0.40 ± 0.04^{b}
Drought [days]	27 ± 8	35 ± 7	51 ± 48	45 ± 11
Flood [days]	44 ± 4^{a}	0 ± 0^{b}	33 ± 7^{a}	0 ± 0^{b}

mid-June 2010 (Table 2). A few days later, the temperature remained above 0°C for a whole day in the hummock tops and bases in both OTCs and CCSs (vegetative season start date; Table 2). In spring 2010, hummock tops had a longer vegetation season for about one week in comparison with bases, probably due to the significantly shorter transition period (Table 2). Summer season temperatures in the OTC hummock tops commonly reached 18–20°C (Fig. 6) and rarely even 30°C. CCS hummock top temperatures were lower, ranging from 12 to 14°C, and rarely reached the maximum of 25°C. Mean maximum and mean summer season temperatures were higher by 7.6°C and 1.6°C, respectively, in the OTC hummock tops compared to the CCS ones (Table 2, Fig. 6). Although the temperature data proved warming effects in the hummock tops in the OTCs, the warming effects were small in the hummock bases. The mean summer seasonal differences between OTC and CCS bases were 0.3°C (OTCs > CCSs). Summer-vegetation season temperatures in the OTC hummock bases reached 8–10°C, while they were slightly lower in CCS bases, being around 7–8°C (Fig. 6). There were no significant differences in mean temperature and mean maximum temperature between OTC and CCS hummock bases (Table 2, Fig. 6). Unfortunately, temperature measurements from the end of summer 2009 and 2010 are not available; however we estimate that temperatures had fallen below 0°C in the second half of October.

Volumetric water content (VWC). — The courses of volumetric water content (VWC) in hummock tops and bases in the OTCs and CCSs, were measured from July 2009 to September 2010 (Fig. 5). At the end of August and beginning of September 2009, the water content dropped slightly in both (OTC and CCS) hummock bases. Both OTC and CCS hummock tops were dry at that time. On September 15–16, 2009, the first frost came and water content in both (OTCs and CCSs) hummock top localities decreased (vegetative season 2009 end date; Table 2). The

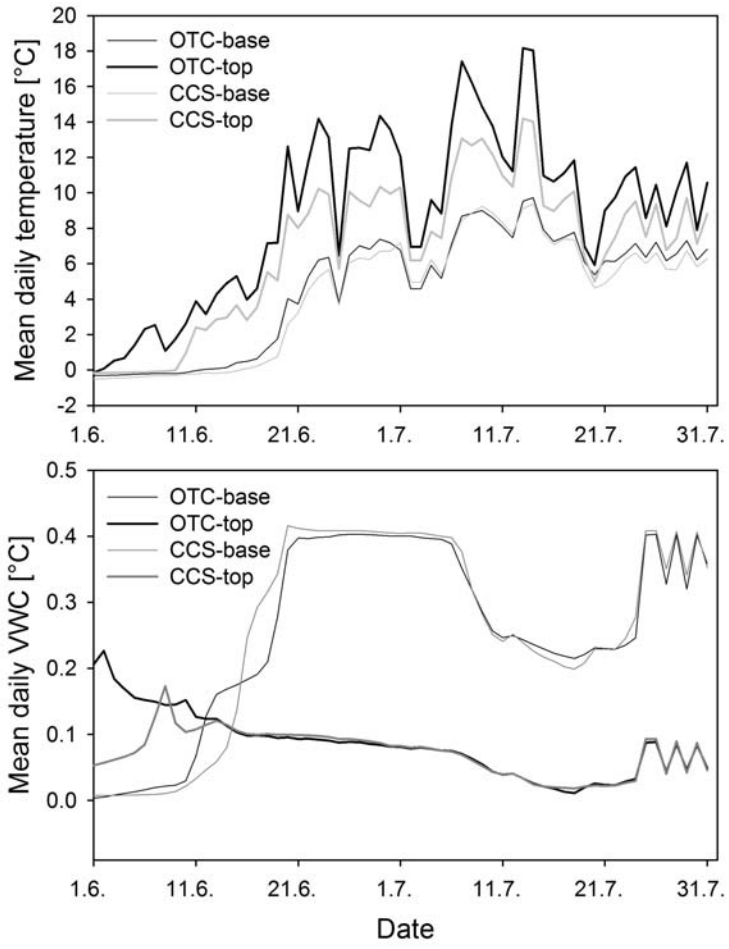

Fig. 6. Mean daily soil temperature and volumetric water content during the first part of the 2010 vegetative season (n = 3 for OTCs, n = 2 for CCSs).

CCS hummock bases froze at the end of September 2009. At that time, the OTC hummock bases still remained unfrozen and froze on October 6 to 8, 2009, with the exception of OTC 1 which froze on December 28, 2009; perhaps the microclimate was kept warmer due to the insulation effect of snow cover. The vegetative season of OTC hummock bases was prolonged by three weeks in comparison with OTC and CCS hummock tops and by one week compared to CCS hummock bases. During winter there were two episodes (mid December 2009 and mid January 2010) when water content in all hummock localities increased because of snow thaw. Snow thaw started in all experimental treatments in the second half of May 2010 (wetting/thawing start date; Table 2). Approximately three days later (wetting/thawing period duration; Table 2), OTC hummock tops were saturated by water (so-called wetting/thawing end date; Table 2).The CCS hummock tops were also

saturated by water in the beginning of June 2010. The thaw started about two weeks later, in mid-June 2010, in the OTC and CCS hummock bases. The maximum saturation levels were reached in the second half of June. A period of drought occurred in July when water content had decreased in all experimental treatments. From that time, the hummock tops (in both OTCs and CCSs) were completely dry till the end of the vegetative season. The hummock bases (in both OTC and CCS) were wetted again at the end of July and water content remained at the same level for the rest of the summer (Fig. 6). Generally, with the exception of the mean maximum VWC reflecting the thaw period in early summer 2010, VWC was always lower in the hummock tops in both OTC and CCSs during both summer seasons (Table 2, Fig. 6). Mean summer season relative water contents in the OTCs and CCSs hummock bases were higher by 0.3 and 0.2 $m^3 m^{-3}$ than in the hummock tops in 2009 and 2010, respectively (Table 2). Affectivity of OTC (warming/increase-decrease relative water content/duration of summer season) is also well documented in detail in the summer curves (Fig. 6).

The annual VWC course seems to be similar in both seasons. After the thaw period and full water saturation in June, a drought period occurred in July and was followed by water re-saturation in August and early September. The high variability reflects the heterogeneity of the microenvironment at the experimental site. Despite this variability, the data indicate that summer 2009 was significantly wetter than that for the same period in 2010. The drought periods, as defined in Table 2, lasted 3 ± 4 days and 21 ± 16 days in 2009 and 2010, respectively (paired t-test, $n = 10$ for each year, $t = -3.364$, $P = 0.005$; only data between July 14, 12:00, and September 12, 10:00 were considered). The large inter-seasonal differences reflect different water availabilities in individual summer seasons.

Ecophysiological parameters of *Nostoc commune* s.l.

Changes in fresh weight of the experimental *Nostoc commune* s.l. colonies during both summer seasons are shown in Fig. 7A, B. The first datapoint in each chart indicates the weight of the colonies in the fully-hydrated state. The colonies were kept in plastic Petri dishes (installed on July 14, 2009) and ECs (installed on July 2, 2010) at hummock bases in the OTC and CCS treatments. At the beginning of summer 2009, shortly after installation of the OTCs and CCSs, the weight of the colonies decreased due to the transfer of the colonies from a well wetted meadow to the Petri dishes, and further due to desiccation of the hummock meadow (see previous chapter). In the first half of August 2009, the weight slightly increased, however it did not reach the weight in the fully-hydrated state as at the beginning of the experiment. The observation in summer 2010 confirmed that the weights of the colonies, in both the Petri dishes and Exposition Chambers, had followed the water availability in the wet meadow (Table 3). No statistical differences were observed between OTCs and CCSs at each date of measurement (Table 3). However, the date on which the measurements were performed, corresponding to the actual conditions at the locality and

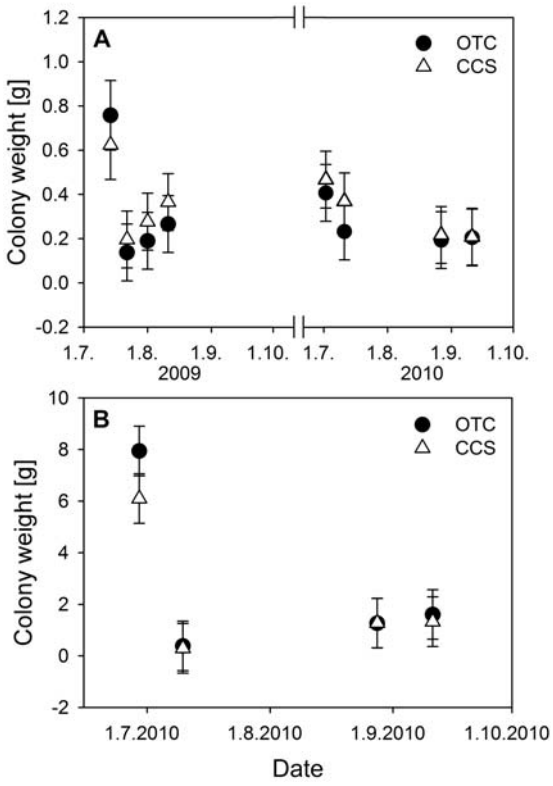

Fig. 7. Changes in *Nostoc commune* s.l. colony weight (mean ± 95% confidence interval) during the vegetation season(s). **A**. Colonies in Petri dishes. **B**. Colonies in Exposition Chambers (n = 9 for each treatment).

the history of these conditions, affected the weight of the colonies (two-way ANOVA, n = 9 for each treatment and exposition type, $F(7,122) = 10.9$, $P < 0.001$ for Petri dishes and $F(3, 64) = 75.9$, $P < 0.001$ for ECs, Fig. 7A,B).

Also F_V/F_M values of *Nostoc commune* indicate the maximum possible quantum yield of the photosystem II, and thus physiological status of the colonies, followed the water availability in the wet meadow (two-way ANOVA, n = 9 for each treatment and exposition type, $F(7,122) = 3.95$, $P = 0.001$ for Petri dishes and $F(3, 64) = 18.4$, $P < 0.001$ for ECs, Fig. 8A, B, Table 3). The maximum F_v/F_m in the fully-hydrated state of the colonies is indicated by the first datapoint in both charts. There were only small differences between OTC and CCS treatments reflecting the similar conditions at hummocks bases in both OTCs and CCSs. However, the F_V/F_M values in the drier summer season of 2010 were slightly higher in comparison with the wetter 2009 season (ANOVA/HSD test for unequal n, n = 54 for 2009 and n = 72 for 2010, $F(1,122) = 19.800$, $P < 0.001$, Table 3). Decrease of F_V/F_M due to meadow desiccation observed in the ECs in 2010 was not confirmed in the Petri dishes, probably due to the experimental setting. The filter paper used for facilita-

Table 3

Physiological chatacteristics (mean ± s.d.) of the *Nostoc* colonies during the 2009 and 2010 growing seasons. The letter indicates homologous groups recognized by Tukey HSD test for P = 0.05. n – number of samples in given treatment, F_V/F_M – maximum quantum yield, NA – nitrogenase activity.

	Weight [g]		F_V/F_M		NA [nmol g^{-1} hr^{-1}]	
	OTC	CCS	OTC	CCS	OTC	CCS
	n = 9	n = 9	n = 9	n = 9	n = 9	n = 9
Petri dishes						
14.7.2009	0.76 ± 0.47^{c}	0.62 ± 0.36^{bc}			3.41 ± 10.66	7.54 ± 12.61
22.7.2009	0.14 ± 0.13^{a}	0.20 ± 0.27^{ab}	0.19 ± 0.10	0.17 ± 0.14	0.00 ± 0.00	0.00 ± 0.00
1.8.2009	0.19 ± 0.11^{a}	0.28 ± 0.16^{ab}	0.14 ± 0.12	0.21 ± 0.13	-3.15 ± 51.07	23.73 ± 22.85
11.8.2009	0.27 ± 0.12^{ab}	0.37 ± 0.20^{abc}	0.25 ± 0.13	0.29 ± 0.12	24.05 ± 35.93	31.42 ± 59.40
2.7.2010	0.41 ± 0.14^{abc}	0.47 ± 0.22^{abc}	0.35 ± 0.09	0.29 ± 0.24	42.37 ± 31.07	24.45 ± 31.86
11.7.2010	0.23 ± 0.08^{ab}	0.37 ± 0.22^{a}	0.33 ± 0.15	0.33 ± 0.19	25.85 ± 32.34	27.54 ± 41.91
27.8.2010	0.19 ± 0.05^{a}	0.22 ± 0.14^{a}	0.33 ± 0.08	0.32 ± 0.21	5.67 ± 9.37	3.66 ± 10.79
10.9.2010	0.21 ± 0.10^{a}	0.21 ± 0.13^{a}	0.31 ± 0.08	0.32 ± 0.14	1.06 ± 9.18	1.28 ± 6.29
Exposition Chambers						
29.6.2010	7.94 ± 2.54	6.10 ± 1.91	0.42 ± 0.06	0.49 ± 0.10	20.81 ± 10.08	18.64 ± 9.14
10.7.2010	0.38 ± 0.13	0.29 ± 0.10	0.13 ± 0.06	0.08 ± 0.16	106.4 ± 285.4	6.63 ± 7.78
28.8.2010	1.27 ± 1.56	1.27 ± 0.90	0.37 ± 0.23	0.42 ± 0.20	13.83 ± 12.44	14.07 ± 11.47
11.9.2010	1.60 ± 1.67	1.33 ± 0.71	0.38 ± 0.10	0.35 ± 0.12	9.39 ± 9.15	6.51 ± 4.72

Table 4

Correlation between environmental variables and *Nostoc* colonies ecophysiological parameters in ECs. The statistically significant correlations are marked by bold font.

	OTC			CCS		
	Weight	F_V/F_M	NA	Weight	F_V/F_M	NA
Temperature	-0.334	**-0.556**	0.198	**-0.594**	**-0.654**	-0.199
	p = 0.088	p = 0.003	p = 0.321	p = 0.009	p = 0.003	p = 0.430
VWC	0.313	**0.447**	0.049	**0.470**	0.228	0.282
	p = 0.111	p = 0.019	p = 0.807	p = 0.049	p = 0.362	p = 0.257
Water level	-0.363	**-0.5749**	0.274	**-0.591**	**-0.596**	-0.258
	p = 0.063	p = 0.002	p = 0.167	p = 0.010	p = 0.009	p = 0.301

tion of water transfer between the dish and the outside environment probably served as a temporary additional water supply to the colonies. Also, the enclosure of the colonies in the Petri dishes reduced evaporation loses compared to the ECs.

The seasonal curves of *N. commune* nitrogenase activity in colonies enclosed in the Petri dishes revealed that this was also related to the water availability in the meadow (two-way ANOVA, n = 9 in each treatment, $F(6,112) = 4.90$, $P < 0.001$, Fig. 9A, B, Table 3). However, great variability of nitrogenase activity among the colonies did not allow detection of any seasonal pattern in the ECs (see the 95% confidential interval of the first datapoint in each chart indicating the values of nitrogenase activity in fully-hydrated colonies). As in the cases of weight and

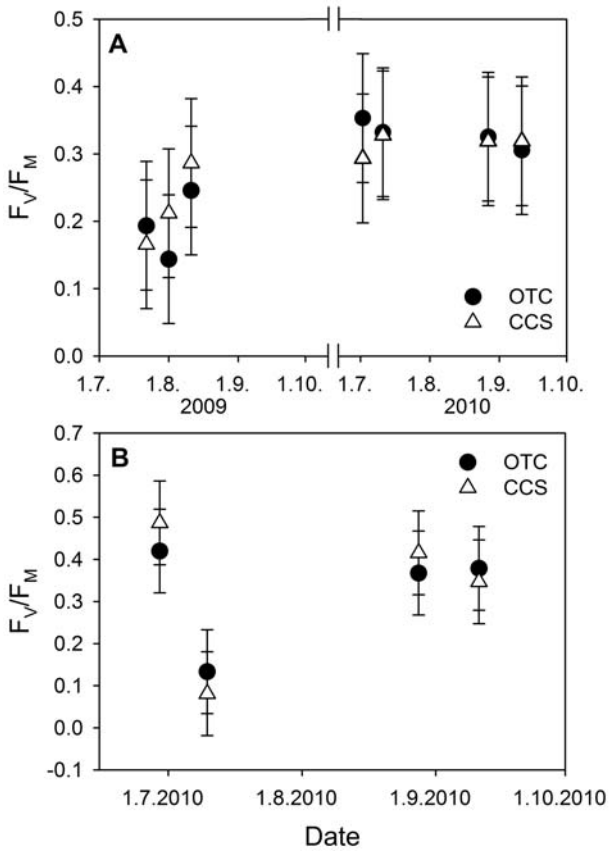

Fig. 8. Changes in *Nostoc commune* s.l. colony maximum quantum yield (F_V/F_M; mean ± 95% confidence interval) during the vegetation season(s). **A**. Colonies in Petri dishes. **B**. Colonies in Exposition Chambers (n = 9 for each treatment).

F_V/F_M, only negligible differences in nitrogenase activity between OTC and CCS treatments were observed.

There was no significant correlation between the microclimate parameters and ecophysiological features of the *Nostoc* colonies kept in Petri dishes in both OTCs and CCSs.

Table 4 shows the correlations between the environmental variables (temperature, VWC and water level depth) and ecophysiological parameters (colony weight, F_V/F_M and NA) of the *Nostoc* colonies kept in ECs, OTCs and CCSs. The nitrogenase activity (NA) was not significantly affected by microclimate parameters for colonies enclosed in ECs or water level depth for colonies enclosed in both OTCs and ECs. However, in OTCs, the F_V/F_M was negatively correlated with temperature and water level depth, but positively with VWC. This was also the case for CCSs in general. However, for the colonies enclosed in the ECs in the CCSs, F_V/F_M was negatively correlated with temperature and colony weight, but positively with VWC.

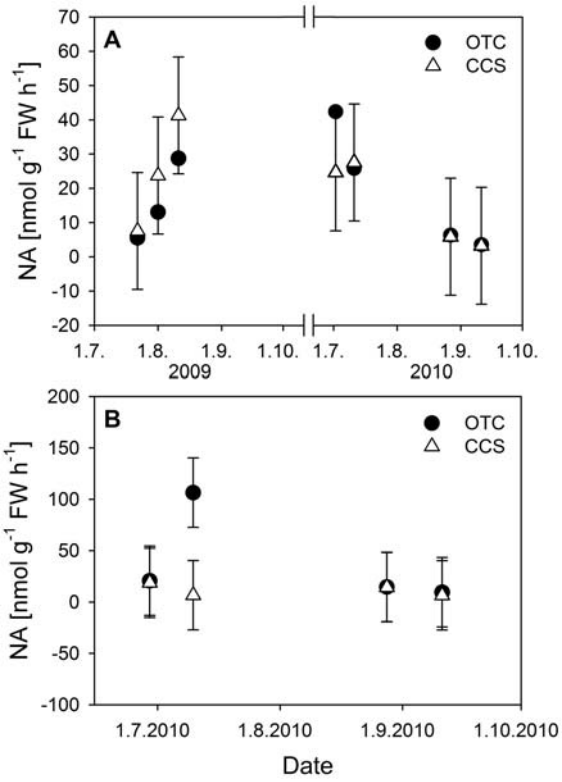

Fig. 9. Changes in *Nostoc commune* s.l. colony nitrogenase activities (NA; mean ± 95% confidence interval) during the vegetation season(s). **A**. Colonies in Petri dishes. **B**. Colonies in Exposition Chambers (n = 9 for each treatment).

These data indicate that the colonies enclosed in Petri dishes were protected from the microclimatic effects, probably due to limited contact between the interior of the Petri dish and its surrounding environment. There may also be a greenhouse effect inside the dish. This type of exposition should not be used in future experiments. The data from the ECs indicate that the colonies were negatively affected by temperature and water deficiency in the meadow; this type of exposition should be preferred in future experiments.

Discussion

Arctic hydro-terrestrial habitats (wetlands, including hummock wet meadows) are important ecosystems in an arid and cold tundra environment (Elster 2002; ACIA 2004). They cover large areas of the Earth's surface and play a fundamental role in the global climate system (Wieder 2001; ACIA 2004). Wet hummock meadows are highly productive plant ecosystems where carbon uptake prevails

above carbon loss from the soil (Rinnan *et al.* 2007; Biasi *et al.* 2008). In addition, the high Arctic hummock wet meadows are a prevalent and highly sensitive type of polar hydro-terrestrial ecosystem affected by climate change (ACIA 2004).

Water level and water physico-chemical parameters

The seasonal courses of climatic and microclimatic conditions of Petuniabukta are discussed in detail in this issue (Láska et. al., this issue). However, from our measurements it is obvious that the range of winter snow accumulation and its melting at the beginning of summer in the upper part of the studied locality is the principal factor influencing water availability in wet meadow hummock tundra. On the contrary, water availability is better balanced at the end of summer probably because of the active layer and melting of the upper part of the permafrost. A similar pattern of seasonal water availability was demonstrated in small tundra lakes in the eastern part of Petuniabukta (Zwolinski *et al.* 2007).

The wet hummock meadow lies on a steplike system of raised marine terrace which is characteristic for the post-Pleistocene shoreline layout of Svalbard (Salvigsen 1984). Geologically, the Petuniabukta area is composed of Middle and Upper carboniferous carbonates, anhydrites, gypsum, sandstone and conglomerates (Dallmann *et al.* 1994). The lower wet hummock meadow terrace is comprised of sandy and gravel sediment originating from local waste material. In previous studies of water physico-chemical parameters of the Petuniabukta freshwater ecosystem (Zwolinski *et al.* 2007; Paluszkiewicz *et al.* 2008; Zwolinski *et al.* 2008) it was shown that marine aerosols, predominantly Na and Cl ions, are commonly present in higher concentrations in the wetland. In our samples, higher Na and Cl contents were recorded only in water inflowing to the meadow from snow melt at the beginning of summer 2009. Yellow-brown precipitates were recorded in both the eastern and western parts of Petuniabukta bay, in the wet meadows and even in shallow pools and lake bottoms, and on the surfaces of mosses, vascular plants and even *Nostoc commune* s.l. mats (Zwolinski *et al.* 2007; Paluszkiewicz *et al.* 2008; Zwolinski *et al.* 2008). Higher concentrations of calcium, magnesium and sulphate in our samples from the experimental field site (compared to inflow water) confirmed their precipitation in the wet hummock meadow. Concentrations of the biogenic elements (N, P) in the inflow water were higher than in the meadow. Hummock wet meadow serves as a biological filter of biogenic elements including CO_2 and serves as a sink for these biogenic elements in the high Arctic ecosystem (Johansson *et al.* 2006; Oberbauer *et al.* 2007).

Microclimatic parameters

Our results and those of several recent studies (Nordstroem *et al.* 2001; Rennermalm *et al.* 2005; Sullivan and Welker 2005; Sullivan *et al.* 2008) clearly demonstrate that, in the hydro-terrestrial environment of wet hummock meadows, the ef-

fect of passive open-top warming chambers clearly depends upon microtopography. The dry tops of hummocks have completely different microclimatic conditions in comparison with wet hummock bases. In addition, there was also a time shift in the warming of dry tops and wet bases of hummocks. *In situ* warming experiments simulated by the OTCs even extended these microclimatic differences.

Because of faster melt inside of the OTC hummock tops, positive temperatures were measured at a depth of ~2 cm below the surface (reached already in mid-May) for several days earlier in the OTCs in comparison with the CCSs. In addition, during melt time the temperature differences between hummock tops in OTC and CCS were as great as 11°C; these differences were not so dramatic later in the season. Similar results of spring temperature differences between warmed and control sites were demonstrated in a moist, acid, tussock tundra site near Toolik Lake, Alaska. Immediately following snow melt in 2002, the differences in soil surface temperatures between warmed and ambient plots approached a maximum of 1.5°C. Later, daily mean temperatures differed by only 0.84°C (Sullivan and Welker 2005).

Mean summer temperatures differed by 1.6°C between OTC and CCS hummock tops. During most of the summer temperatures in the OTC hummock tops were at 18–20°C and rarely reached 30°C, while in the control boxes they were 12–14°C and rarely 25°C. Mean maximum temperatures were higher by 7.6°C in OTC hummock tops than in control boxes. On the contrary, the warming effect was much lower in the wet bases of hummock in the OTC treatments with mean summer differences between hummock bases in OTCs and CCSs were 0.3°C. Summer temperatures in hummock bases reached 8–10°C in OTCs and 7–8°C in CCSs. Temperature differences between hummock tops and bases reached 8–10°C in OTCs and 4–6°C in CCSs treatments. Although the ITEX warming open top chambers were used very commonly in various Arctic, Antarctic and alpine terrestrial ecosystems (Marion *et al.* 1997; Hollister and Webber 2000; Kudo and Suzuki 2002; Wada *et al.* 2002; Bokhorst *et al.* 2008; Walker *et al.* 2008; Rinnan *et al.* 2009a; Rinnan *et al.* 2009b; Simmons *et al.* 2009), the OTC warming experiments are more rare in various shallow wetland habitat types (Nordstroem *et al.* 2001; Rennermalm *et al.* 2005; Sullivan and Welker 2005; Sullivan *et al.* 2008). In NW Greenland wetlands (Sullivan *et al.* 2008), the microtopography of the sites is a mosaic of hummocks, which extend above the water table, and hollows, which lie beneath 5–15 cm of water during the short growing season. Air temperature (20 cm above surface) in OTC was about 2°C higher than in the control. Hummock soil temperature was higher than air temperature. Hollows temperature was colder than air temperature. Midday soil temperatures were generally warmer in hummocks than in hollows. These results principally follow our data and characterize the warming effects of OTC in a wetland ecosystem (high Arctic wet meadows).

A wide spectrum of ecological and physiological studies have shown that, in terms of environmental priorities, demands for moisture (water in a liquid form)

precede demands for nutrients, which in turn, precede demands for high temperatures (Svoboda and Henry 1987; Kennedy 1993; Elster 2002; Elster and Benson 2004). The courses of volumetric water content showed that OTC hummock bases remained unfrozen until October or even December. The vegetative season of OTC hummock bases was prolonged by one and/or three weeks in comparison with OTC and CCS hummock tops, and CCS hummock bases. Episodes with snow thaw can occur even during winter, meaning that liquid water can be available for poikilohydric biota (ecological opportunists) living in wet meadows.

Ecophysiological parameters of *Nostoc commune* s.l.

Desiccation stress represent the most severe injury in the polar regions (Davey 1989). Cyanobacterial primary production and nitrogen fixation have to follow the moisture conditions (Liengen and Olsen 1997; Vincent 2000; Novis *et al.* 2007; Kvíderová *et al.* 2011). However, Davey (1989), Hawes *et al.* (1992), Novis *et al.* (2007) and Kvíderová *et al.* (2011) have shown that even a partially hydrated *Nostoc commune* s.l. colony is capable of photosynthesis and nitrogen fixation in Arctic hydroterrestrial habitats. This can provide a big advantage for *Nostoc commune* s.l. itself and also for the ecological functioning of the hummock meadows when water supply fluctuates widely. *In situ* experiments at the same locality showed that if colony water loss was less than ca 40% of its fully hydrated weight, no or only minor desiccation damages were observed. However, when weight loss exceeded ca 40%, the colony starts to shrink and changes in the mucilage structure begins. Nitrogenase activity declined slowly when water loss exceeded 70% and diminished completely at a weight loss of ca 80%. The photochemical activity remained unaffected till the colonies lost *ca* 80% of their original weight and was detectable till weight loss of ca 90% (Kvíderová *et al.* 2011). However, measurements in summer 2010 confirmed that weights of *Nostoc commune* s.l. colonies, their maximum quantum yield of photosystem II, and thus physiological status of the colonies and their nitrogenase activity in both Petri dishes and Exposition Chambers followed the water availability in the wet meadow. No statistical differences were observed between OTCs and CCSs at each date of measurement, probably due to only small differences in the microclimatological parameters at hummock bases in the OTCs and CCSs. Our *in situ* one and/or two seasons warming experiments consisting of passive open-top chambers, which raise ambient temperature and slightly changed water availability in experimental treatments of wet hummock meadow tundra, did not influence the photochemical processes and nitrogenase activity of *Nostoc commune* s.l. colonies.

Proposition for further research

Ecosystem manipulation of the wet meadow where *Nostoc commune* s.l. colonies produce high biomass in the wet bases of hummocks resulted in mean summer

temperature being only 0.3°C higher in OTCs than control treatments. However, short-term snow-thaw episodes occurred in the OTCs during winter. Earlier snow melt in the spring and later freezing over in fall also significantly prolong the vegetation season (by several days/weeks) in the manipulated environment of the OTCs. Liquid water is available for the growth of *Nostoc* colonies during this time. However, we do not have photochemistry and nitrogenase activity measurements in the non-vegetation season. On the basis of our results and experiences of this pilot study of *Nostoc commune* s.l. ecophysiological reaction to simulated warming, we propose the following research:

- Continuous whole year measurements of the ecophysiological parameters of *Nostoc* colonies, which may show growth of *Nostoc* colonies during the non-vegetation season.
- Continue with OTC manipulation using the same technique and measure the ecophysiological response of *Nostoc* colonies to warming over a long period of time (5 to 10 years experiment).
- Technical adjustment of OTCs with the aim of increasing the temperature by up to 3 to 5°C at the hummock bottom. This can be done by covering the OTC's (with the same material by which the OTCs are constructed), with creation of holes. The number and size of holes should be prepared according to an OTC's temperatures.
- Replacement of the Petri dishes by more open exposition chambers like our ECs or direct fixation of a colony to the substrate by a wire mesh. The Petri dishes, even with drilled holes, are not suitable for such experiments, since the transport of water and heat between the interior of the Petri dish and surrounding environment is restricted.

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References

ACIA. 2004. *Impacts of warming climate: Arctic climate impact assessment*. Cambridge University Press, Cambridge: 1039 pp.

BIASI C., MEYER H., RUSALIMOVA O., HÄMMERLE R., KAISER C., BARANYI C., H. D., LASHCHINSKY N., BARSUKOV P. and RICHTER A. 2008. Initial effect of experimental warming on carbon exchange rates, plant growth and microbial dynamics of a lichen-rich dwarf shrub tundra in Siberia. *Plant and Soil* 307: 191–205.

BOKHORST S., HUISKES A., CONVEY P., VAN BODEGOM P.M. and AERTS R. 2008. Climate change effects on soil arthropod communities from the Falkland Islands and the Maritime Antarctic. *Soil Biology & Biochemistry* 40: 1547–1556.

CALLAGHAN T.V., BJÖRN L.O., CHERNOV Y., CHAPIN T., CHRISTENSEN T.R., HUNTLEY B., IMS R.A., JOHANSSON M., JOLLY D., JONASSON S., MATVEYEVA N., PANIKOV N., OECHEL W., SHAVER G., ELSTER J., HENTTONEN H., LAINE K., TAULAVUORI K., TAULAVUORI E. and ZÖCKLER C. 2004a. Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. *Ambio* 33: 404–417.

CALLAGHAN T.V., BJÖRN L.O., CHERNOV Y., CHAPIN T., CHRISTENSEN T.R., HUNTLEY B., IMS R.A., JOHANSSON M., JOLLY D., JONASSON S., MATVEYEVA N., PANIKOV N., OECHEL W., SHAVER G., ELSTER J., JONSDOTTIR I.S., LAINE K., TAULAVUORI K., TAULAVUORI E. and ZÖCKLER C. 2004b. Responses to projected changes in climate and UV-B at the species level. *Ambio* 33: 418–435.

CHAPIN F.S.I. and SHAVER G.R. 1985. Individualistic growth response of tundra plant species to environmental manipulation in the field. *Ecology* 66: 564–576.

CONVEY P., PUGH P.J.A., JACKSON C., MURRAY A.W., RUHLAND C.T., XIONG F.S. and DAY T.A. 2002. Response of Antarctic terrestrial microarthropods to long-term climate manipulation. *Ecology* 83: 3130–3140.

DALLMANN W.K., OHTA Y., BIRJIKOV A.S., KARMOUSHENKO E.P. and SIROTKIN A.N. 1994. *Geological map of Svalbard 1:100000, sheet C7G Dicksonfjorden.* Norsk Polarinstitut.

DAVEY M.C. 1989. The effects of freezing and desiccation on photosynthesis and survival of terrestrial Antarctic algae and cyanobacteria. *Polar Biology* 10: 29–36.

DAVEY M.C. and ROTHERY P. 1992. Factors causing the limitation of growth of terrestrial algae in maritime Antarctic during late summer. *Polar Biology* 12: 595–601.

DAY T.A., RUHLAND C.T., GROBE C.W. and XIONG F. 1999. Growth and reproduction of Antarctic vascular plants in response to warming and UV radiation reductions in the field. *Oecologia* 119: 24–35.

ELSTER J. 2002. Ecological classification of terrestrial algal communities in polar environments. *In*: L. Beyer and M. Bötler (eds) *Geoecology of Antarctic ice-free coastal lanscapes*. Springer-Verlag, Berlin, Heidelberg: 303–326.

ELSTER J. and BENSON E.E. 2004. Life in the polar terrestrial environment with a focus on algae and cyanobacteria. *In*: B.J. Fuller, N. Lane and E.E. Benson (eds) *Life in the frozen state*. CRC Press, Boca Raton, London, New York, Washington, D.C.: 111–150.

ELSTER J., SVOBODA J. and KANDA H. 2001. Controlled environmental platform used in temperature manipulation study of a stream periphyton in the Ny-Ålesund, Svalbard. *In*: J. Elster, J. Seckbach, W.F. Vincent and O. Lhotský (eds) *Algae and extreme environments*. Cramer, Stuttgart: 63–75.

HAWES I., HOWARD-WILLIAMS C. and VINCENT W. 1992. Desiccation and recovery of Antarctic cyanobacterial mats. *Polar Biology* 12: 587–594.

HENRY G.H.R. and SVOBODA J. 1986. Dinitrogen fixation (acetylene reduction) in high Arctic sedge meadow communities. *Arctic and Alpine Research* 18: 181–187.

HOLLISTER R.D. and WEBBER P.J. 2000. Biotic validation of small open-top chambers in a tundra ecosystem. *Global Change Biology* 6: 835–842.

HOWARD C.S. 1933. Determination of total dissolved solids in water analysis. *Industrial & Engineering Chemistry Analytical Edition* 5: 4–6.

JOHANSSON T., MALMER N., CRILL P.M., FRIBORG T., AKERMAN J.H., MASTEPANOV M. and CHRISTENSEN T.R. 2006. Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing. *Global Change Biology* 12: 2352–2369.

KARLBERG B. and TWENGSTROM S. 1983. Application based on gas diffusion and flow injection analysis. *Focus* 6: 14.

KENNEDY A.D. 1993. Water as a limiting factor in the Antarctic terrestrial environment: A biogeographical synthesis. *Arctic, Antarctic and Alpine Research* 25: 308–315.

KENNEDY A.D. 1995. Antarctic terrestrial ecosystem response to global environmental change. *Annual Review of Ecology and Systematics* 26: 683–704.

KUDO G. and SUZUKI S. 2002. Warming effects on growth, production, and vegetation structure of alpine shrubs: a five-year experiment in northern Japan. *Oecologia* 135: 280–287.

KVÍDEROVÁ J., ELSTER J. and ŠIMEK M. 2011. *In situ* response of *Nostoc commune* s.l. colonies to desiccation in Central Svalbard, Norwegian High Arctic. *Fottea* 11: 87–97.

LIENGEN T. and OLSEN R.A. 1997. Nitrogen fixation by free-living cyanobacteria from different coastal sites in a High Arctic tundra, Spitzbergen. *Arctic and Alpine Research* 29: 470–477.

MADSEN B.C. and MURPHY R.J. 1981. Flow injection and photometric determination of sulfate in rainwater with methylthymol blue. *Analytical Chemistry* 53: 1924–1926.

MARION G.M., HENRY G.H.R., FRECKMAN D.W., JOHNSTONE J., JONES G., JONES M.H., LÉVESQUE E., MOLAU U., MØLGAARD P., PARSONS A.N., SVOBODA J. and VIRGINIA R.A. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology* 3: 20–32.

MAXWELL B. 1992. Arctic climate: Potential for change under global warming. *In*: F.S.I. Chapin, R.L. Jeffries, J.F. Reynold, G.R. Shaver and J. Svoboda (eds) *Arctic esosystems in a changing climate*. Academic Press, San Diego: 11–34.

MAXWELL K. and JOHNSON G.N. 2000. Chlorophyll fluorescence – a practical guide. *Journal of Experimental Botany* 51: 659–668.

MOLAU U. and MØLGAARD P. (eds) 1996. *ITEX manual (2nd. edition)*. Danish Polar Centre, Copenhagen: 85 pp.

NORDSTROEM C., SOEGAARD H., CHRISTENSEN T.R., FRIBORG T. and HANSEN B.U. 2001. Seasonal carbon dioxide balance and respiration of a high-arctic fen ecosystem in NE-Greenland. *Theoretical and Applied Climatology* 70: 149–166.

NOVIS P.M., WHITEHEAD D., GREGORICH E.G., HUNT J.E., SPARROW A.D., HOPKINS D.W., ELBERLING B. and GREENFIELD L.G. 2007. Annual terrestrial fixation in terrestrial populations of *Nostoc commune* (Cyanobacteria) from an Antarctic dry valley is driven by temperature. *Global Change Biology* 13: 1224–1237.

OBERBAUER S.F., TWEEDIE C.E., WELKER J.M., FAHNESTOCK J.T., HENRY G.H.R., WEBBER P.J., HOLLISTER R.D., M.D. W., KUCHY A., ELMORE E. and STARR G. 2007. Tundra CO_2 fluxes in response to experimental warming across latitudinal and moisture gradient. *Ecological Monographs* 72: 221–238.

PALUSZKIEWICZ R., MAZUREK M., RACHLEWICZ G. and ZWOLIŃSKI Z. 2008. Hydrogeochemia zagłębień tundrowych na podniesionych terasach morskich, Petuniabukta, Spitsbergen Środkowy [Hydrogeochemistry of tundra basins on the raised marine terraces, Petuniabukta, Central Spitsbergen]. *In*: A. Kowalska and J. Pereyma (eds) *Środowisko przyrodnicze obszarów polarnych*. Uniwersytet im. Adama Mickiewicza, Poznań: 141–149.

PARSONS L.R. and BANDARANAYAKE W.M. 2009. Performance of a new capacitance soil moisture probe in a sandy soil. *Soil Science Society of America Journal* 73: 1378–1385.

PAUL E.A. and CLARK F.E. 1996. *Soil microbiology and chemistry*. Academic Press, Toronto: 340 pp.

PROCTOR C.M. and HOOD A.R. 1954. Determination of phosphate in sea water by an iso-butanol extraction procedure. *Journal of Marine Research* 13: 112–132.

RENNERMALM A.K., SOEGAARD H. and NORDSTROEM C. 2005. Interannual variability in carbon dioxide exchange from a high Arctic fen estimated by measurements and modeling. *Arctic, Antarctic and Alpine Research* 37: 545–556.

RINNAN R., MICHELSEN A., BÅÅTH E. and JONASSON S. 2007. Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. *Global Change Biology* 13: 28–39.

RINNAN R., ROUSK J., YERGEAZ E., G.A. K. and BÅÅTH E. 2009a. Temperature adaptation of soil bacterial communities along an Antarctic climate gradient: predicting responses to climate warming. *Global Change Biology* 15: 2615–2625.

RINNAN R., STARK S. and TOLVANEN A. 2009b. Responses of vegetation and soil microbial communities to warming and simulated herbivory in a subarctic heath. *Journal of Ecology* 97: 788–800.

ROHÁČEK K. and BARTÁK M. 1999. Technique of the modulated chlorophyll fluorescence: basic concepts, useful parameters, and some applications. *Photosynthetica* 37: 339–363.

ROLPH S.G. 2003. *Effects on a ten-year climate warming experiment on nitrogen cycling in the high arctic tundra*. MSc. thesis, University of British Columbia, Vancouver: 61 pp.

RŮŽIČKA J. and HANSEN E.H. 1981. *Flow injection analysis*. John Wiley, New York: 528 pp.

RŮŽIČKA J., STEWART J.W.B. and ZAGATTO E.A. 1976. Flow injection analysis: Part IV. Stream sample splitting and its application to the continuous spectrophotometric determination of chloride in brackish waters. *Analytica Chimica Acta* 81: 387–396.

SALVIGSEN O. 1984. Occurrence of pumice on raised beaches and Halocene shoreline displacement in the inner Isfjorden area, Svalbard. *Polar Research* 2: 107–113.

SHAVER G.R., CANADELL J., CHAPIN F.S.I., GUREVITCH J., HARTE J., HENRY G.H.R., INESON P., JONASSON S., MELILLO J., PITELKA L. and RUSTAD L. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. *Bioscience* 50: 871–882.

SIMMONS B.L., WALL D.H., ADAMS B.J., AYRES E., BARRETT J.E. and VIRGINIA R.A. 2009. Long-term experimental warming reduces soil nematode populations in the McMurdo Dry Valleys, Antarctica. *Soil Biology & Biochemistry* 41: 2052–2060.

SOKOLOFF V.P. 1933. Water of crystallization in total solids of water analysis. *Industrial & Engineering Chemistry Analytical Edition* 5: 336–337.

STEWART W.D.P., FITZGERALD G.P. and BURRIS R.H. 1967. *In situ* studies of N_2 fixation using the acetylene reduction technique. *Proceedings of the National Academy of Sciences of the United States of America* 58: 2071–2073.

STRATHDEE A.T. and BALE J.S. 1993. A new cloche design for evaluating temperature in polar terrestrial ecosystem. *Polar Biology* 13: 577–580.

SULLIVAN P., ARENS S., CHIMNER R. and WELKER J. 2008. Temperature and microtopography interact to control carbon cycling in a High Arctic fen. *Ecosystems* 11: 61–76.

SULLIVAN P.F. and WELKER J.M. 2005. Warming chambers stimulate early season growth of an Arctic sedge: results of a minirhizotron field study. *Oecologia* 142: 616–626.

SVOBODA J. and HENRY G.H.R. 1987. Succession in marginal Arctic environments. *Arctic, Antarctic and Alpine Research* 4: 373–384.

VINCENT W.F. 2000. Cyanobacterial dominance in the Polar Regios. *In*: B.A. Whitton and M. Potts (eds) *The ecology of cyanobacteria.* Kluwer Academic Publishers, Dordrecht: 321–340.

WADA N., SHIMONO M., M. M. and KOJINA S. 2002. Warming effects on shoot development growth and biomass production in sympatric evergreen alpine dwarf shrub *Empetrum nigrum* and *Loiseleuria procumbens*. *Ecological Research* 17: 125–132.

WALKER J.K.M., EGGER K.N. and HENRY G.H.R. 2008. Long-term experimental warming alters nitrogen-cycling communities but site factors remain the primary drivers of community structure in high Arctic tundra soil. *The ISME Journal* 2: 982–995.

WIEDER R.K. 2001. Past, present and future peatland carbon balance: an empirical model based on ^{210}Pb-dated cores. *Ecological Applications* 11: 327–342.

ZWOLINSKI Z., MAZUREK M., PALUSZKIEWICZ R. and RACHLEWICZ G. 2008. The matter fluxes in the geoecosystem of small tundra lakes, Petuniabukta coast, Billefjorden, Central Spitsbergen. *Zeitschrift für Geomorphologie* (Suppl. 1) 52: 79–101.

ZWOLINSKI Z., RACHLEWICZ G., MAZUREK M. and PALUSZKIEWICZ R. 2007. The geoecological model for small tundra lakes, Spitzbergen. *Landform Analysis* 5: 113–118.

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