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Nitrogen fixation and diurnal changes of photosynthetic activity in Arctic soil crusts at different development stage

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ABSTRACT

Nitrogen fixation and photosynthesis provided by microbial phototrophs (cyanobacteria and eukaryotic microalgae) are important processes occurring in Arctic soil crusts. Here, we describe and compare these processes in biological soil crusts from Central Svalbard at different stages of development. The gradient from poorly-developed to well-developed soil crusts was accompanied by the changes in biovolume of microbial phototrophs, nitrogenase and photosynthetic activity. The lowest biovolume of microbial phototrophs was detected in poorly-developed soil crusts as a consequence of the initial stage of soil colonization. The biovolume initially increased during the soil crust development but decreased in well-developed lichenized soil crusts. However, nitrogenase activity decreased from poorly to more developed soil crusts. Diurnal courses of photosynthetic activity differed among the soil crust types showing shifts in diurnal minima and maxima; the poorly-developed soil crust reacted faster to changes in temperature and PAR. In spite of different microclimatic conditions during the measurements, temperature was the main factor influencing photosynthetic activity while the effect of PAR was not significant. Higher temperatures led to inhibition of photosynthetic activity and increased energy dissipation, indicating acclimation/adaptation of the soil crust photosynthetic microorganisms to a cold environment.

1. Introduction

Biological soil crusts are one of the most important components in Arctic desert and semi desert ecosystems [1]. These crusts consist of soil particles held together by the main soil crust components such as microbial phototrophs (the term includes both cyanobacteria and eukaryotic microalgae), fungi, mosses, liverworts and lichens [2]. Soil crust organisms provide important processes for the Arctic desert and semi desert ecosystems, for instance, atmospheric nitrogen fixation as a source of nitrogen and photosynthesis as a source of organic carbon, and hence energy, for consumers and decomposers [3].

Low temperature, lack of water and high photosynthetically active radiation (PAR, 400–700 nm)/UV-radiation are typical stressors in the extreme polar environments where biological soil crusts are frequently present [1,4]. These factors inhibit biological processes and cause changes in diversity, abundance and ecophysiological performance of soil crust communities in the upper layers of soil crusts [5–7]. However, soil crust microbial phototrophs, due to a diverse range of ecological and physiological life strategies, manifest an ability to tolerate stressful conditions [1]. For example, the heterocystous cyanobacteria *Scytonema* sp. and *Nostoc* sp, produce the dark yellowish pigment scytonemin in their sheaths which acts as an UV-screen [8]. These taxa consequently can survive on the soil surface, and are the organisms primarily responsible for the darkening of the soil surface associated with biological soil crusts [9]. Another strategy to avoid or minimize stressful conditions is vertical migration of filaments beneath the soil surface. This behavior is typical for cyanobacteria from the order Oscillatoriales, because they are capable of a gliding movement and can achieve a balance between receiving sufficient light for photosynthesis and avoiding harmful UV radiation and photooxidation [10,11]. Similarly to cyanobacteria, eukaryotic microalgae, e.g. *Klebsormidium* sp. and *Zygnema* sp., form multi-layered structures or are interwoven within the upper millimeters of soil for protection from UV radiation [12,13]. Increased PAR/UV radiation causes serious damage to photosystem II (PSII) in

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photosynthetic microorganisms and, hence, decreased photosynthetic efficiency [14]. The depression of photosynthetic efficiency usually occurs at midday [15]. Thus, the prolonged day during the summer season in the Arctic results in decreased photosynthetic activity [16]. These changes occur rapidly, either due to short-term oscillations caused by clouds, or due to diurnal irradiance cycles. Therefore, variable chlorophyll fluorescence-based approaches may provide valuable data on changes in photosynthetic activity [16]. For detailed and rapid insight into the light energy utilization, i.e. either its utilization in photosynthetic reactions, or its dissipation as heat, the chlorophyll fluorescence fast-transient analysis (OJIP transient) seems to be suitable [17]. Moreover, knowledge of the diurnal changes in photosynthetic activity is crucial to establish reliable primary productivity models [18].

Soil crust community composition and abundance varies depending on the disturbance rate (water-wind erosion, soil cryodisturbance, anthropogenic activities, animal grazing, etc.) from poorly-developed to well-developed soil crusts [19]. Although the process of soil crust development in time and space has been described [2], little is known about the factors driving small scale patterns of soil crust community structure and associated ecological processes. The poorly-developed soil crusts usually have low nutrient content and low abundance of microbial phototrophs dominated by cyanobacteria. These soil crusts are light in colour and have low capability to mitigate damage caused by UV radiation. In the next step of development mosses and lichens begin to appear and the soil crusts acquire darker colour due to higher abundance of microbial phototrophs which increase net photosynthetic exchange rates. In the latest development stage moss and soil lichen crusts form mosaic patterns with higher small-scale variation [20].

Here, we hypothesized that composition and biovolume of microbial phototrophs and associated ecological processes (photosynthesis and nitrogenase activity) might follow the gradient of soil crust development in the High Arctic. Moreover, we studied how individual environmental parameters (soil temperature and PAR) influence photosynthetic (expressed as variable chlorophyll fluorescence parameters) and nitrogenase activities as proxies of primary production and nitrogen fixation, with respect to diurnal cycles. Since the application of the OJIP transient measurement is proposed as possible approach for study of photosynthetic processes, for the first time we applied it in the Artic soil crusts correlating the shared parameter (maximum quantum yield) with the standard protocol.

2. Materials and methods

2.1. Field site description and sampling

The sampling sites were located in the vicinity of Petunia Bay, the northwestern branch of Billefjorden, Dickson Land, Svalbard. Soil crusts cover a substantial part of the area. The mean annual air temperature is approximately −6.5 °C. An active period when liquid water is available normally starts in June and lasts until the end of August or middle of September (90–100 days) with mean soil temperatures of 4–6 °C and air temperatures of 5–7 °C [23].

The field experiments and sample collection were conducted in the end of July (for sites SC1 and SC2) and the beginning of August (for sites SC3 and SC4) 2013. Soil crusts were selected in the field (area of 5 × 5 m per each site) based on their distinct macroscopic features and represented gradient (from poorly-developed to well developed) based on chemical parameters and cyanobacterial community composition listed in Table 1 [19]. Pictures of studied soil crusts and their detailed description including soil chemistry have been already presented in a previous publication [19].

In order to determine the effect of environmental factors on the photosynthetic activity of biological soil crusts, temperature and photosynthetically active radiation (PAR) were measured at the soil surface in each sampling site. The soil temperature was measured using Minikin T dataloggers (Environmental Monitoring Systems, Czech Republic) positioned on the soil crust surface. PAR was measured using a PU-550 light meter (Metra Blansko, Czech Republic) equipped with a custom-made quantum probe.

After measurements of photosynthetic activity in the field, the same soil crust samples (diameter of 1 cm, depth of 2 cm, weight of around 4 g) were collected and brought to the Czech Station in Svalbard to measure nitrogenase activity. After that, samples were placed into new zip bags, kept at −20 °C and transported in dry ice to the Czech Republic.

2.2. Biovolume of microbial phototrophs in soil crusts

Biovolume of microbial phototrophs in soil crusts was estimated by light and epifluorescence microscopy (Olympus BX 51). A non-staining method was employed using chlorophyll autofluorescence according to Kaštovská et al. [6]. 1 g of soil was diluted in 4 ml of distilled water and mixed thoroughly. A total of 20 μl of the soil solution was used for the microscopy. Filter cube (Olympus, MWB) with blue excitation at 450–480 nm (emission 515 + nm) was tested for eukaryotic microalgae and filter cube (Olympus, MWG) with green excitation at 510–550 nm (emission 590 + nm) was tested for cyanobacteria in soil crust samples. However, due to coarse soil texture it was not possible to distinguish eukaryotic microalgal cells by the filter with blue excitation. Thus, only the filter with green excitation was used, which allowed the identification of cyanobacteria into three groups according to their cell morphology: unicellular, filamentous and heterocystous cyanobacteria. Under this filter it was also possible to distinguish diatoms and coccoid microalgae (green algae Chlorophyta and yellow-green algae Xanthophyceae) within the eukaryotic microalgae. Basic geometric equations for cylinders with hemispherical ends and spheres were applied to calculate the biovolume per soil samples.

Table 1
Sampling sites description is taken from the previous publication [19].

Site	GPS coordinates	Soil crust description	Chemical parameters				The most relatively abundant cyanobacterial species
			pH	Corg, %	N-NH_4, μg kg^{-1}	Water content, %	
SC1	78° 40′ 57″ N 16° 26′ 39″ E	Poor-developed, light-colored, no lichen presence	8.1	4.8	3.5	19.6	*Leptolyngbya* sp., *L. antarctica*, *L. subtilissima*, *Coleofasciculus chthonoplastes*
SC2	78° 41′ 31″ N 16° 26′ 47″ E	Mid-developed, brown, with presence of lichens	8.0	11.5	4.0	30.8	*Leptolyngbya* sp., *L. antarctica*, *L. nostocorum*, *Calothrix* sp.
SC3	78° 41′ 36″ N 16° 26′ 12″ E	Mid-developed, brown, with presence of lichens	7.8	15.6	5.7	35.3	*Leptolyngbya* sp., *L. nostocorum*, *Stigonema ocellatum*, *Nostoc* sp.
SC4	78° 41′ 54″ N 16° 26′ 22″ E	Well-developed, dark-colored, dense lichen cover	7.5	16.9	3.4	34.5	*Phormidium* sp., *Leptolyngbya* sp., *Leptolyngbya nostocorum*