Ecophysiological Response Against Temperature in *Klebsormidium* (Streptophyta) Strains Isolated From Biological Soil Crusts of Arctic and Antarctica Indicate Survival During Global Warming

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Global warming, as global problem, may particularly affect the vegetation of the Polar Regions. Biological soil crusts (BSCs) as pioneer communities perform a variety of important ecological functions under the harsh environmental conditions at high latitudes. The green algal genus *Klebsormidium* is a common member of BSCs and in the present study, the ecophysiological resilience to temperature stress of 20 strains from Arctic and Antarctica were investigated. All 20 *Klebsormidium* strains exhibited the capability to grow under a wide temperature range (from 6 to 28°C) and hence were characterized as psychrotolerant with optimum growth temperatures between 18°C and 26°C. Statistical analyses showed no significant differences in optimum growth temperature. However, growth rates at optimal temperatures varied between strains and indicated infraspecific physiological plasticity. Furthermore, correlation with the sampling sites as well as different BSC types were examined but no significance was confirmed. Our results revealed that Polar *Klebsormidium* strains are able to survive such changing conditions, and even benefit from higher environmental temperatures.

**Keywords:** Aeroterrestrial algae, growth, ecophysiology, temperature stress, Polar Regions

**INTRODUCTION**

Biological soil crusts (BSCs) are complex agglomerations formed by diverse phototrophic and heterotrophic organisms such as microalgae, cyanobacteria, lichens, bryophytes, bacteria, microfungi and microfauna (Belnap, 2006; Darby and Neher, 2016). These pioneer communities constitute the dominant vegetation cover on the temporarily snow- and ice-free soil surfaces of the Polar Regions and perform a wealth of ecological functions (Yoshitake et al., 2010; Williams et al., 2016). BSCs stabilize soil against water and wind erosion as well as cryoturbation, contribute to primary production, carbon and nitrogen fixation and benefit the growth of vascular plants (Belnap, 2002; Eldridge and Greene, 1994; Evans and Johansen, 1999; Yoshitake et al., 2010).
The filamentous green alga genus *Klebsormidium* (Klebsormidiophyceae, Streptophyta) can be found worldwide in numerous habitats (Elster et al., 2008; Škaloud and Rindi, 2013) and is also commonly associated with BSCs in both the Arctic and Antarctica (Hayashi and Shinozaki, 2012; Pushkareva et al., 2016; Borghardt et al., 2017a,b; Rippin et al., 2018). This genus has a pivotal role in the formation of BSCs by its filamentous morphology as well as excretion of extracellular polymeric substances (EPS), which promote the moisture retention and stabilization of the soil surface (Barberousse et al., 2006; Hu et al., 2009; Bödö et al., 2016).

The Polar Regions are characterized by harsh environmental conditions such as low temperatures, a pronounced seasonality, scarcity of liquid water and strong solar radiation, and *Klebsormidium* has the potential to cope with these stressors (Elster et al., 2008; Karsten and Rindi, 2010; Kaplan et al., 2012; Holzinger and Karsten, 2013; Kitzing et al., 2014). The ecophysiology of *Klebsormidium* has been studied on several strains from different biogeographically regions (e.g., Holzinger et al., 2014; Herburger and Holzinger, 2015; Blaas and Holzinger, 2017; Donner et al., 2017). It is known that members are poikilohydric, which describes the inability to actively regulate cellular water content. Therefore, organisms nearly completely dehydrated (Holzinger et al., 2014; Karsten and Holzinger, 2014). The electron transport chains in the thylakoid membranes are affected by cellular desiccation and inhibit photosynthesis (De Winder et al., 1990; Gray et al., 2007; Fernández-Marin et al., 2016). However, studies on Arctic and Antarctic *Klebsormidium* strains showed resistance against desiccation induced injuries and investigation on alpine strain of *Klebsormidium crenulatum* revealed molecular mechanisms such as up-regulation of photosynthetic transcripts caused by dehydration (Elster et al., 2008; Holzinger et al., 2014). Furthermore, strains accumulate osmolytes (raffinose and sucrose), free amino acids (γ-aminobutyric acid) and starch grains and oil droplets in order to retain water within the cells and protect against membrane damage and protein aggregation, which also caused by freezing (Bisson and Kirt, 1995; Manabu et al., 2008; Holzinger et al., 2014). However, the knowledge on the capabilities of Polar *Klebsormidium* strains to cope with increasing temperatures due to the climate change is insufficient.

Climate change is already happening. An increase of annual mean temperature of more than 1°C was determined in the Polar Regions in the last decades and the atmospheric temperature in the Artic has doubled since 1980 (Kejna et al., 2013). Mean air temperature of Antarctic King George Island was −4.3°C in 1959, while only −1.1°C was measured in 2008 (Kejna et al., 2013). It is presumed that the BSCs of the Polar Regions cannot resist the rapid climate change, and hence their composition as well as distribution will shift or BSCs will even be displaced by invasive species (Frenot et al., 2005; Pushkareva et al., 2016). Previous results of a pedological analysis of polar BSC species showed no significant influences of C, N, S, TP (total phosphorus) and pH. In addition, a statistically significant influence of precipitation on species composition was determined (Borghardt et al., 2017b). Therefore, studies on ecophysiological performance of Polar strains not only merit a particular attention but also urgently needed. Findings, whether and how Arctic and Antarctic *Klebsormidium* strains cope with higher temperatures, might enable to predict the development of this key vegetation in the Polar Regions under the climate change scenarios.

**MATERIALS AND METHODS**

**Study Sites**

Biological soil crusts samples were collected at Svalbard (Arctic) and King George Island as well as Ardley Island (South Shetland Islands, Antarctic Peninsula, Figure 1 and Table 1). Crust material was cut out of the soil surface using plastic petri dishes (60 mm φ) and a spatula. BSCs were air dried with open lids to avoid mold growth and stored in paper bags at a dark place.

The archipelago Svalbard located in the Arctic Ocean ranges from 74 to 81° north latitude and from 10 to 35° east longitude. Svalbard has a mild climate compared to regions at the same latitudes because of the West Spitsbergen Current (WSC), which transports warm Atlantic water masses into the Arctic Ocean along the West coast. The mean temperature in summer is 7 and −14°C (minimum −35°C) in winter (Norwegian Meteorological Institute)1.

King George Island and the nearby Island Ardley belong to the South Shetland Islands, which are located in maritime Antarctica (61 to 63° south latitude, 54 to 63° west longitude). The archipelago is separated from the Antarctic Peninsula by the Bransfield Strait and from South America by the Drake Passage. Because of the Antarctic Circumpolar Current (ACC) the maritime Antarctica has milder climate with mean annual temperature of −2.5°C on King George (Kejna et al., 2013).

**Algal Isolates and Cultivation**

Biological soil crusts samples were cultured on 1.5% Difco™ Agar (Becton Dickonson GmbH, Heidelberg, Germany) enriched with Bold’s basal medium with vitamins (Starr and Zeikus, 1993) modified by tripled nitrate concentration (3N-MBBM + V). To obtainunalgal isolates enrichment cultures were regularly screened for colonies using stereo microscope (ZS40, Olympus, Tokyo, Japan) with a magnification of 40-fold. Potential microalgal colonies were isolated from the enrichment cultures with a needle and transferred to a new agar plate. The growth of colonies was frequently monitored with the stereo microscope and several sub-isolates were generated for further purification. If no contamination with concomitant microalgae or fungi was detected the isolate was transferred to a new agar plate under sterile conditions. Strains were identified using light microscope (BX-51, Olympus, Tokyo, Japan) following the identification key of Ettl and Gärtner (2014) and descriptions by Rindi et al. (2011) as well as Mikhailyuk et al. (2014). Nine Antarctic Klebsormidium strains and eleven Arctic strains were isolated and part of the Culture Collection at the University of Rostock. One strain (CCALA 708) was delivered from the Culture Collection of Autotrophic

1https://www.met.no
Organisms (CCALA, Institute of Botany, Charles University, Toebø, Czechia).

Isolates were cultured at 15°C and 35 μmol photons m⁻² s⁻¹ (Daylight Lumilux Cool White lamps L36W/840, OSRAM Licht AG, Munich, Germany) under a 16:8 h light-dark cycle.

Growth in Response to Temperature
For *in vivo* measurement of the effect of 12 different temperatures on growth, as temperature gradient from 6, 8, 10, 12, 13, 14, 17, 18, 20, 23, 26 to 28°C, chlorophyll *a* fluorescence was used as a proxy for biomass accumulation according to Gustavs et al. (2009). Growth experiments were carried out using a modified self-constructed algal incubator (Kunststoff-Technik GmbH, Rostock, Germany) as described in Woelfel et al. (2014), with the possibility to create a temperature gradient at 35 μmol photons m⁻² s⁻¹ (LED) under a 16:8 light-dark cycle. All measurements were always done with log-phase cultures, which were pre-incubated at experimental conditions for 10 days. Pre-cultures were inoculated with 100 μl of liquid stock culture and were kept on 24 well plates. Each well was filled with 2.5 ml
3N-BBM-agar (Starr and Zeikus, 1993; BBM modified by the addition of triple nitrate concentration). After 10 days a small amount of pre-culture biomass was transferred into a new 24-well plate with four replicates for each strain. Chlorophyll \( a \) fluorescence was measured (excitation 440 nm, emission 680 nm, top read function) each day with a SpectraMax M2e multiplate reader (MPR; Molecular Devices, Biberach, Germany) using the software SoftMax Pro version 5.4 (Molecular Devices, LLC, San Jose, CA, United States). Dark-incubation of 10 min was performed in order to open all reaction centers of photosystem II before starting each measurement. Increasing fluorescence was detected as relative fluorescence units (RFUs) and the fluorescence measured directly after the inoculation serving as a starting value. Each strain was tested four times. Calculation of growth rate for each of the four replicates was performed according to the well-established protocol by Gustavs et al. (2009). Fluorescence \( F_t \) at a given time point \( t \) are calculated as \( F_t = F_0 \exp(\mu t) \) with \( F_0 \) as initial fluorescence and \( \mu \) (d\(^{-1}\)) as growth rate in the respective time interval. For the calculation of \( \mu \) the measured chlorophyll \( a \) fluorescence values were fitted with the equation described above. The fitting was based on the sum of the mean square error \( A_{\text{RFU}} \) which was calculated as 
\[
A_{\text{RFU}} = (F_t - F_{t, \text{cal}})^2 
\]
with \( F_t \) as fluorescence at a given point in time and \( F_{t, \text{cal}} \) (RFU) as calculated fluorescence at a given point in time with five subsequent fluorescence values. \( A_{\text{RFU}} \) was minimized by the Microsoft Excel add-in Solver with the model “GRG- non-linear.” Optimum growth rate was defined as growth rate values >80% according to Gustavs et al. (2010).

**Multivariate Statistics**

Multivariate analysis was conducted using the statistical programs PRIMER 6. Non-metric multi-dimensional scaling (MDS, Kruskal and Wish, 1978) was based on square root transformed data and Bray-Curtis similarity and the significance of similarity was tested by using ANOSIM permutation test (Clarke and Green, 1988; Clarke, 1993).

**RESULTS**

The results showed a wide range in the capability to grow with increasing temperatures in all investigated Klebsormidium strains (6–28°C, Figure 2). All strains grew at minimum temperature of 6°C but only four strains were able to grow at the maximum temperature of 28°C (AD-16a K. nitens, EiE-15a K. dissectum, AB01-2b K. montanum, AB01-13a K. klebsii). Two growth patterns along the temperature gradient were observed and can be characterized as a plateau-like growth optimum and a more pronounced, sharp optimum. AB01-2b K. montanum, EiE-14a K. subtile, Hinter-11II K. crenulatum, Hinter-15a K. dissectum, EiE-15a K. dissectum, and AD-16a K. nitens exhibited a plateau-like growth optimum, whereas EiE-1B K. subtile, Björn-1C K. subtile and AB01-1D K. dissectum showed a more pronounced, sharp optimum. Conspicuous differences in optimum growth temperature of K. montanum and K. dissectum strains indicated an infraspecific physiological plasticity. Growth rates at optimal temperatures of K. montanum varied between 18 and 26°C. Both strains were isolated from Antarctic BSCs. Similar individual growth pattern was observed in K. dissectum strains, which exhibit optimum growth temperatures between 18 and 23°C. All investigated K. dissectum strains were found in Arctic biocrust communities. An overview of the optimum growth temperatures of all strains is presented in Figure 3. The MDS analysis and ANOSIM test (global \( R \) value = 0.01, \( p = 0.424 \)) show neither significant grouping by Polar Regions nor by species (Figure 4).

**DISCUSSION**

The investigated Polar Klebsormidium strains exhibited relatively high optimum growth temperatures between 18 and 26°C and

| Strain | Species | Station number | Coordinates |
|--------|---------|----------------|-------------|
| Bjom1C | Klebsormidium cf. | 1 | 78°13.167’N 15°18.777’E |
| Bjom1a | Klebsormidium cf. | 2 | 78°11.180’N 15°45.662’E |
| EE1B   | Klebsormidium cf. | 3 | 78°10.292’N 16°00.574’E |
| EE-14a | Klebsormidium cf. | 4 | 78°10.205’N 16°01.336’E |
| EE-15a | Klebsormidium cf. | 5 | 78°54.434’N 12°00.158’E |
| Hinter-11ll | Klebsormidium cf. | 6 | 78°54.434’N 12°00.158’E |
| Hinter-15a | Klebsormidium cf. | 7 | 62°12.765’S 58°55.886’W |
| AB01-1all | Klebsormidium cf. | 8 | 62°12.775’S 58°56.816’W |
| AB01-2b | Klebsormidium cf. | 9 | 62°13.315’S 58°57.289’W |
| AB01-13a | Klebsormidium cf. | 10 | 62°13.315’S 58°57.289’W |
| AB01d  | Klebsormidium cf. | 11 | 62°13.315’S 58°57.289’W |
| AB01m  | Klebsormidium cf. | 12 | 62°13.315’S 58°57.289’W |
FIGURE 2 | Continued

![Graphs showing ecophysiological response against temperature in Klebsormidium species.](image)
FIGURE 2 | Median growth rate $\mu$ [d$^{-1}$] as response against temperature of all 20 Klebsormidium strains. Error bars mark maximum and minimum growth rates of the four replicates for the respective temperature. The temperature range of a few strains were a little different, please keep in mind the y-axis.
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**FIGURE 3** | Overview of the optimum growth temperatures of all 20 Klebsormidium strains. Light blue = Antarctic strains, dark blue = Arctic strains.

hence, were characterized as rather psychrotolerant taxon than as a psychrophilic or even cryophilic alga. Psychrotolerant organisms grow optimally at 20 to 25°C but are able to survive at temperatures below 0°C (Morita, 1975). Psychrophiles *sensu stricto* have a growth optimum temperature at <15°C and cryophilic organisms prefer temperatures below −10°C (Morita, 1975; Elster, 1999). Both Arctic and Antarctic Klebsormidium strains showed wide ranges of temperatures. Ubiquitous distribution of Klebsormidium is known and it can be concluded that members seem to be ecophysiological generalists with eurythermal growth response pattern. Most of the strains exhibit optimum temperature of 20°C, which coincides with former literature values from the Alps (20°C, Karsten et al., 2010; Karsten and Holzinger, 2012). Furthermore, results presented in this study were comparable with findings on Klebsormidium strains from other biogeographical regions, such as America (median 19°C, Donner et al., 2017) and Germany (20°C, Karsten and Rindi, 2010), and strengthen the hypothesis. Further data on the temperature requirements for growth in both closely related genera of the Klebsormidiophyceae Interfilum, Entransia as well as Hormidiella and other green algae are rare or still missing.

The Arctic Svalbard has a more fluctuating climate with higher summer and lower winter temperatures compared to the Antarctic South Shetland Islands. Furthermore, noticeable
environmental differences between the Arctic and Antarctica based on their cold water and low temperature history were reported (Zacher et al., 2009). Antarctica has a much longer cold water history of about 23 Mio. years, while the geological cold water history of the Arctic is still younger (ca. 2 Mio years, Sabbe et al., 2003). However, this environmental differences could not be linked to the findings presented in this study because there are no significant differences between Antarctic and Arctic strains. In addition, BSCs microalgae such as Klebsormidium have to cope with microclimatic factors, which might explain the local as well as infraspecific differences of optimum growth temperatures.

The differences between the optimum growth temperatures and the air temperatures in the Polar Regions (average 7°C in Svalbard) initially seem to be large. However, investigations on vegetation mats in Svalbard, which described potentially BSCs, revealed an increase by 35% of the temperatures within the vegetation mats (Coulson et al., 1993). These findings constitute a rise by about 5°C during summertime and caused by heat emission due to biological activity (Coulson et al., 1993). These higher temperatures within BSCs in general might explain the ascertained optimum growth temperatures of Klebsormidium strains.

A temperature increase up to 7.7°C is predicted for the Arctic region, which will lead to a decline of snow cover and glacier retreat. Our findings indicated that Polar Klebsormidium strains are able to survive such changing conditions. Consequently, it allows to presume that Polar Klebsormidium strains might benefit from higher environmental temperatures and colonies will increase. This is already indicated by the conspicuously high abundance of Klebsormidium species in Arctic as well as Antarctic BSCs (Elster et al., 1999; Kaštovská et al., 2005; Borchhardt et al., 2017a,b, 2018).

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/supplementary material.

AUTHOR CONTRIBUTIONS

SG-P performed the experiments and analyzed the data. NB collected the samples, cultivated and isolated Klebsormidium strains, identified species, performed experiments, analyzed data, created figures and table, and wrote the first draft of the manuscript. Both authors edited and revised the manuscript and approved the publication.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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