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

Nadine Borchhardt* and Sigrid Gründling-Pfaff

Applied Ecology and Phycology, Institute of Biological Science, University of Rostock, Rostock, Germany

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; Borchhardt 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; Büdel 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-Marín 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 Kirst, 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 (Borchhardt 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 Artic 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 Ø) 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[TM] 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 obtain unialgal 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
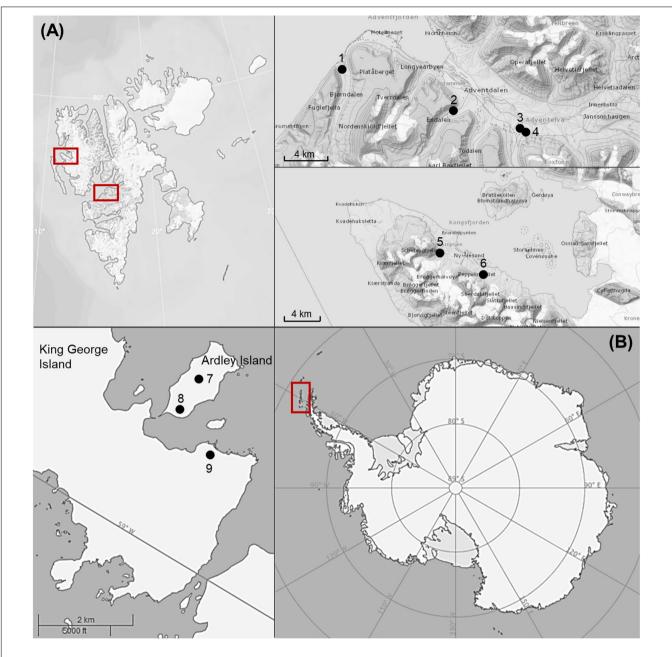
---

[1]https://www.met.no

FIGURE 1 | Map of sampling areas for collected biological soil crusts. **(A)** The two investigated sampling localities on Arctic Svalbard (around Ny-Alesund and Longyearbyen), **(B)** The two investigated sampling localities on Antarctic South Shetland Islands (Ardley and King George Island). Numbers of sampling stations are explained in **Table 1**.

Organisms (CCALA, Institute of Botany, Charles University, Tøeboò, 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

TABLE 1 | Overview of used *Klebsormidium* strains including sampling stations on Arctic Svalbard and Antarctic King George and Ardley Island.

Strain	Species	Station number	Coordinates
Björn1C	*Klebsormidium* cf. *subtile*	1 (Björndalen)	78°13.167″N 15°18.777″E
Björn-11a	*Klebsormidium* cf. *crenulatum*	1 (Björndalen)	78°13.167″N 15°18.777″E
EiE1B	*Klebsormidium* cf. *subtile*	2 (Eindalen entrance)	78°11.180″N 15°45.662″E
EiE-14a	*Klebsormidium* cf. *Subtile*	2 (Eindalen entrance)	78°11.180″N 15°45.662″E
EiE-15a	*Klebsormidium* cf. *Dissectum*	2 (Eindalen entrance)	78°11.180″N 15°45.662″E
ADC1H	*Klebsormidium* cf. *klebsii*	3 (Adventsdalen, camp)	78°10.292″N 16°00.574″′E
AD-14a	*Klebsormidium* cf. *subtile*	4 (Adventsdalen)	78°10.205″N 16°01.336″E
AD-16a	*Klebsormidium* cf. *nitens*	4 (Adventsdalen)	78°10.205″N 16°01.336″E
CCALA708	*Klebsormidium* cf. *montanum*	5 (subglacial)	78(°55.480(N 11°46.408″E
Hinter-11aII	*Klebsormidium* cf. *Crenulatum*	6 (beneath outback plateau)	78°54.434″N 12°00.156″E
Hinter-15a	*Klebsormidium* cf. *dissectum*	6 (beneath outback plateau)	78°54.434″N 12°00.156″E
A1-1a	*Klebsormidium* cf. *flaccidum*	7 (Ardley)	62°12.765″S 58°55.888″W
A1-2a	*Klebsormidium* cf. *Montanum*	7 (Ardley)	62°12.765″S 58°55.888″W
A4II2b	*Klebsormidium* cf. *flaccidum*	7 (Ardley)	62°12.765″S 58°55.888″W
APII2b	*Klebsormidium* cf. *flaccidum*	8 (Ardley Palaeo)	62°12.775″S 58°56.816″W
AB01-1aII	*Klebsormidium* cf. *flaccidum*	9 (King George)	62°13.315″S 58°57.289″W
AB01-2b	*Klebsormidium* cf. *montanum*	9 (King George)	62°13.315″S 58°57.289″W
AB01-13a	*Klebsormidium* cf. *klebsii*	9 (King George)	62°13.315″S 58°57.289″W
AB01d	*Klebsormidium* cf. *dissectum*	9 (King George)	62°13.315″S 58°57.289″W
AB01m	*Klebsormidium* cf. *montanum*	9 (King George)	62°13.315″S 58°57.289″W

*Station numbers 1–6, Arctic study site; station numbers 7–9, Antarctic study site. For comparison see also the map of **Figure 1**.*

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 in 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, LCC, 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 Ft at a given time point t are calculated as $F_t = F_0 e^{\mu t}$ with F_0 as initial fluorescence and μ (d^{-1}) as growth rate in the respective time interval. For the calculation of μ 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_{Fl} which was calculated as $A_{Fl} = (F_t - F_{t,cal})^2$ with F_t (RFU) as fluorescence at a given point in time t and $F_{t,cal}$ (RFU) as calculated fluorescence at a given point in time t with five subsequent fluorescence values. A_{Fl} 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).
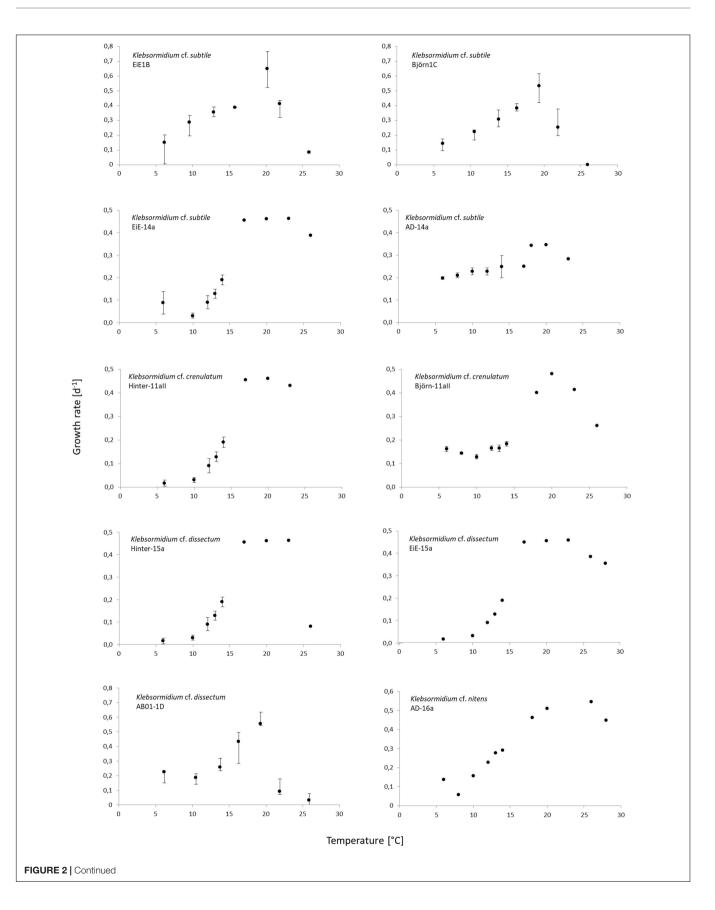
Multivariate Statistics

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).
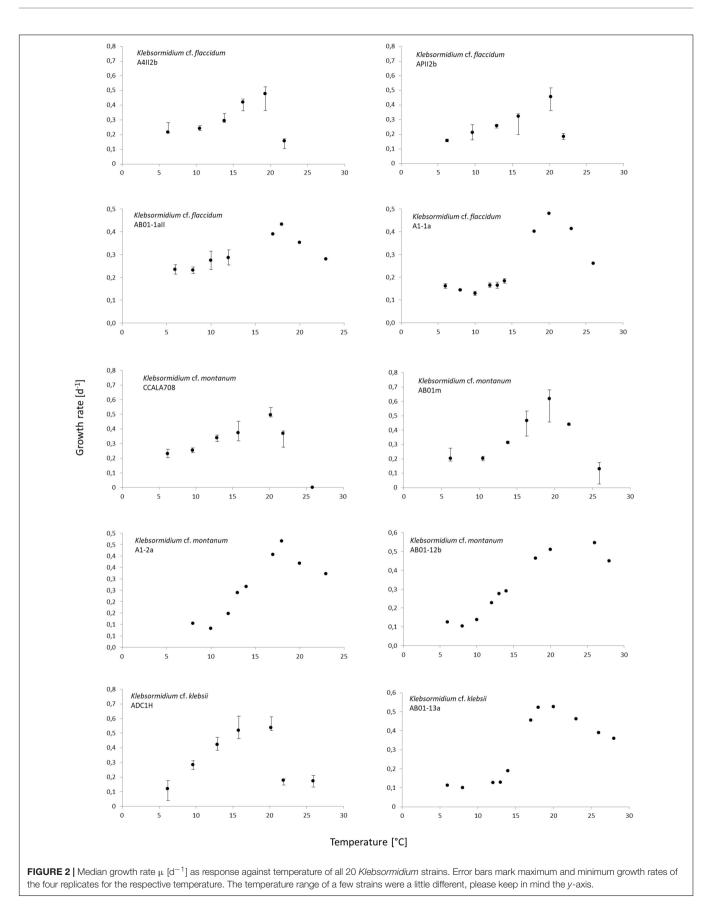
RESULTS

The results showed a wide range in the capability to growth 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-11aII *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**).
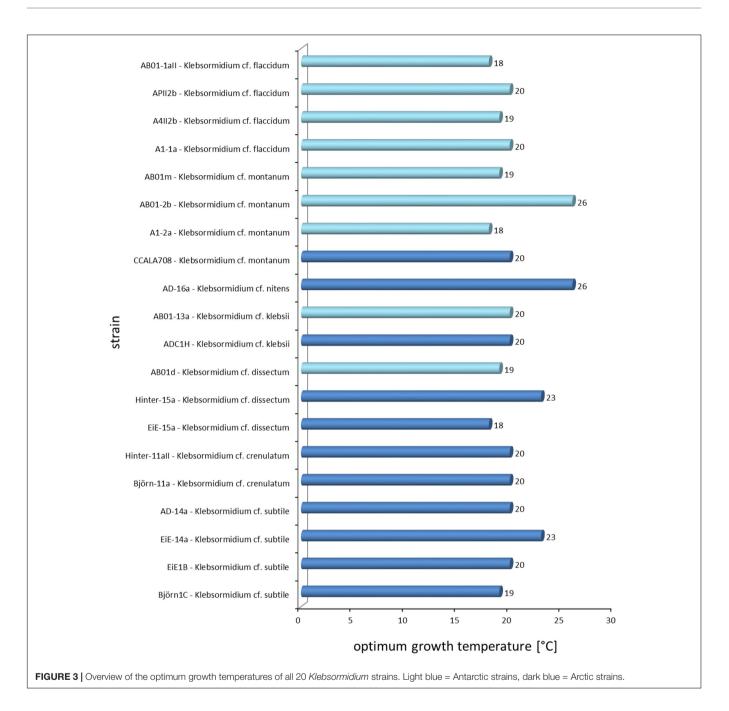
DISCUSSION

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

FIGURE 2 | Continued

FIGURE 2 | Median growth rate μ [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.

FIGURE 3 | Overview of the optimum growth temperatures of all 20 *Klebsormidium* strains. Light blue = Antarctic strains, dark blue = Arctic strains.
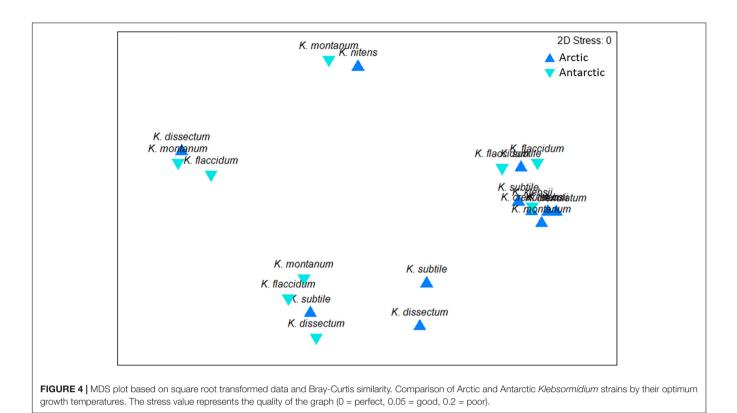
hence, were characterized as rather psychrotolerant taxon than as a psychrophilic or even cryophilic alga. Psychrotolerant organisms grow optimally at 20 to 25°C but are able to survive at temperatures below 0°C (Morita, 1975). Psychrophiles *sensu stricto* have a growth optimum temperature at <15°C 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

FIGURE 4 | MDS plot based on square root transformed data and Bray-Curtis similarity. Comparison of Arctic and Antarctic *Klebsormidium* strains by their optimum growth temperatures. The stress value represents the quality of the graph (0 = perfect, 0.05 = good, 0.2 = poor).

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.

FUNDING

ACKNOWLEDGMENTS

REFERENCES

Barberousse, H., Ruiz, G., Gloaguen, V., Lombardo, R. J., Djediat, C., Mascarell, G., et al. (2006). Capsular polysaccharides secreted by building façade colonisers: characterisation and adsorption to surfaces. *Biofouling* 22, 361–370. doi: 10.1080/08927010601035803

Belnap, J. (2002). Nitrogen fixation in biological soil crusts from southeast Utah, USA. *Biol. Fertil. Soils* 35, 128–135. doi: 10.1007/s00374-002-0452-x

Belnap, J. (2006). The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrol. Process.* 20, 3159–3178. doi: 10.1002/hyp.6325

Bisson, M. A., and Kirst, G. O. (1995). Osmotic acclimation and turgor pressure regulation in algae. *Naturwissenschaften* 82, 461–471. doi: 10.1007/BF01131597

Blaas, K., and Holzinger, A. (2017). F-actin reorganization upon de- and rehydration in the aeroterrestrial green alga *Klebsormidium crenulatum. Micron* 98, 34–38. doi: 10.1016/j.micron.2017.03.012

Borchhardt, N., Baum, C., Mikhailyuk, T., and Karsten, U. (2017a). Biological soil crusts of Arctic Svalbard - water availability as controlling factor for microalgal biodiversity. *Front. Microbiol.* 8:1485. doi: 10.3389/fmicb.2017.01485

Borchhardt, N., Baum, C., Thiem, D., Köpcke, T., Karsten, U., Leinweber, P., et al. (2018). Soil microbial phosphorus turnover and identity of algae and fungi in biological soil crusts along a transect in a glacier foreland. *Eur. J. Soil Biol.* 91, 9–17. doi: 10.1016/j.ejsobi.2018.12.006

Borchhardt, N., Schiefelbein, U., Abarca, N., Boy, J., Mikhailyuk, T., Sipman, H. J. M., et al. (2017b). Diversity of algae and lichens in biological soil crusts of Ardley and King George islands, Antarctica. *Antarct. Sci.* 9, 1–9. doi: 10.1017/S0954102016000638

Büdel, B., Dulić, T., Darienko, T., Rybalka, N., and Friedl, T. (2016). *Cyanobacteria and Algae of Biological Soil Crusts. In Biological Soil Crusts: An Organizing Principle in Drylands.* Berlin: Springer International Publishing, 55–80.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143. doi: 10.1111/j.1442-9993.1993.tb00438.x

Clarke, K. R., and Green, R. H. (1988). Statistical design and analysis for a 'Biological Effect' study. *Mar. Ecol. Prog. Ser.* 46, 213–226.

Coulson, S., Hodkinson, I. D., Strathdee, A., Bale, J. S., Block, W., Worland, M. R., et al. (1993). Simulated climate change - the interaction between vegetation type and microhabitat temperatures At Ny-Alesund, Svalbard. *Polar Biol.* 13, 67–70.

Darby, B. J., and Neher, D. A. (2016). Microfauna within biological soil crusts. *Ecol. Stud.* 226, 139–157. doi: 10.1007/978-3-319-30214-0_8

De Winder, B., Matthius, H. C., and Mur, L. R. (1990). The effect of dehydration and ion stress on carbon dioxide fixation in drought-tolerant phototrophic microorganisms. *FEMS Microbiol. Lett.* 74, 33–38. doi: 10.1111/j.1574-6941.1990.tb01669.x

Donner, A., Glaser, K., Borchhardt, N., and Karsten, U. (2017). Ecophysiological response on dehydration and temperature in terrestrial *Klebsormidium* (Streptophyta) isolated from biological soil crusts in central european grasslands and forests. *Microb. Ecol.* 73, 850–864. doi: 10.1007/s00248-016-0917-913

Eldridge, D., and Greene, R. (1994). Microbiotic soil crusts - a review of their roles in soil and ecological processes in the rangelands of Australia. *Aust. J. Soil Res.* 32:389. doi: 10.1071/SR9940389

Elster, J., Degma, P., Kováčik, L., Valentová, L., Šramková, K., and Batista Pereira, A. (2008). Freezing and desiccation injury resistance in the filamentous green alga *Klebsormidium* from the Antarctic, Arctic and Slovakia. *Biologia* 63, 843–851. doi: 10.2478/s11756-008-0111-112

Elster, J., Lukesová, A., Svoboda, J., Kopecky, J., and Kanda, H. (1999). Diversity and abundance of soil algae in the polar desert, Sverdrup Pass, central Ellesmere Island. *Polar Rec.* 35:231. doi: 10.1017/S0032247400015515

Ettl, H., and Gärtner, G. (2014). *Syllabus der Boden-, Luft- und Flechtenalgen.* Berlin: Springer.

Evans, R. D., and Johansen, J. R. (1999). Microbiotic crusts and ecosystem processes. *Crit. Rev. Plant. Sci.* 18, 183–225. doi: 10.1080/07352689991309199

Fernández-Marín, B., Holzinger, A., and García-Plazaola, J. (2016). "Photosynthetic strategies of desiccation-tolerant organisms," in *Handbook of Photosynthesis*, ed. M. Pessarakli (Boca Raton, FL: CRC Press), 663–681. doi: 10.1201/9781315372136-36

Frenot, Y., Chown, S. L., Whinam, J., Selkirk, P. M., Convey, P., Skotnicki, M., et al. (2005). Biological invasions in the Antarctic: extent, impacts

and implications. *Biol. Rev.* 80, 45–72. doi: 10.1017/S1464793104006542

Gray, D. W., Lewis, L. A., and Cardon, Z. G. (2007). Photosynthetic recovery following desiccation of desert green algae (Chlorophyta) and their aquatic relatives. *Plant Cell Environ.* 30, 1240–1255. doi: 10.1111/j.1365-3040.2007.01704.x

Gustavs, L., Schumann, R., Eggert, A., and Karsten, U. (2009). In vivo growth fluorometry: accuracy and limits of microalgal growth rate measurements in ecophysiological investigations. *Aquat. Microb. Ecol.* 55, 95–104. doi: 10.3354/ame01291

Gustavs, L., Eggert, A., Michalik, D., and Karsten, U. (2010). Physiological and biochemical responses of green microalgae from different habitats to osmotic and matric stress. *Protoplasma* 243, 3–14. doi: 10.1007/s00709-009-0060-9

Hayashi, Y., and Shinozaki, A. (2012). Visualization of microbodies in *Chlamydomonas reinhardtii. J. Plant Res.* 125, 579–586. doi: 10.1007/s10265-011-0469-z

Herburger, K., and Holzinger, A. (2015). Localization and quantification of callose in the streptophyte green algae zygnema and *Klebsormidium*: correlation with desiccation tolerance. *Plant Cell Physiol.* 56, 2259–2270. doi: 10.1093/pcp/pcv139

Holzinger, A., and Karsten, U. (2013). Desiccation stress and tolerance in green algae: consequences for ultrastructure, physiological and molecular mechanisms. *Front. Plant Sci.* 4:327. doi: 10.3389/fpls.2013.00327

Holzinger, A., Kaplan, F., Blaas, K., Zechmann, B., Komsic-Buchmann, K., and Becker, B. (2014). Transcriptomics of desiccation tolerance in the streptophyte green alga *Klebsormidium* reveal a land plant-like defense reaction. *PLoS One* 9:e110630. doi: 10.1371/journal.pone.0110630

Hu, S.-P., Zhou, Y., Zhang, L., Zhu, X.-D., Li, L., Luo, L.-J., et al. (2009). Correlation and quantitative trait loci analyses of total chlorophyll content and photosynthetic rate of rice (*Oryza sativa*) under water stress and well-watered conditions. *J. Integr. Plant Biol.* 51, 879–888. doi: 10.1111/j.1744-7909.2009.00846.x

Kaplan, F., Lewis, L., Wastian, J., and Holzinger, A. (2012). Plasmolysis effects and osmotic potential of two phylogenetically distinct alpine strains of *Klebsormidium* (Streptophyta). *Protoplasma* 249, 789–804. doi: 10.1007/s00709-011-0324-z

Karsten, U., and Holzinger, A. (2012). Light, temperature, and desiccation effects on photosynthetic activity, and drought-induced ultrastructural changes in the green alga *Klebsormidium dissectum* (Streptophyta) from a High Alpine Soil Crust. *Microb. Ecol.* 63, 51–63. doi: 10.1007/s00248-011-9924-6

Karsten, U., and Holzinger, A. (2014). Green algae in alpine biological soil crust communities: acclimation strategies against ultraviolet radiation and dehydration. *Biodivers. Conserv.* 23, 1845–1858. doi: 10.1007/s10531-014-0653-652

Karsten, U., Lütz, C., and Holzinger, A. (2010). Ecophysiological performance of the aeroterrestrial green alga *Klebsormidium crenulatum* (charophyceae, streptophyta) isolated from an alpine soil crust with an emphasis on desiccation stress. *J. Phycol.* 46, 1187–1197. doi: 10.1111/j.1529-8817.2010.00921.x

Karsten, U., and Rindi, F. (2010). Ecophysiological performance of an urban strain of the aeroterrestrial green alga *Klebsormidium* sp. (Klebsormidiales, Klebsormidiophyceae). *Eur. J. Phycol.* 45, 426–435. doi: 10.1080/09670262.2010.498587

Kaštovská, K., Elster, J., Stibal, M., and Santrůcková, H. (2005). Microbial assemblages in soil microbial succession after glacial retreat in Svalbard (high arctic). *Microb. Ecol.* 50, 396–407. doi: 10.1007/s00248-005-0246-244

Kejna, M., Arazny, A., and Sobota, I. (2013). Climatic change on King George Island in the years 1948–2011. *Polish Polar Res.* 34, 213–235. doi: 10.2478/popore

Kitzing, C., Pröeschold, T., and Karsten, U. (2014). UV-induced effects on growth, photosynthetic performance and sunscreen contents in different populations of the green alga *Klebsormidium fluitans* (Streptophyta) from alpine soil crusts. *Microb. Ecol.* 67, 327–340. doi: 10.1007/s00248-013-0317-x

Kruskal, J. B., and Wish, M. (1978). Multidimensional scaling. *Soc. Sci.* 11, 19–34.

Manabu, N., Kenji, M., Matsuo, U., Nagao, M., Matsui, K., and Uemura, M. (2008). *Klebsormidium flaccidum*, a charophycean green alga exhibits cold acclimation that is closely associated with compatible solute accummation and ultrastructural changes. *Plant Cell Environ.* 31, 872–885. doi: 10.1111/j.1365-3040.2008.01804.x

Mikhailyuk, T., Holzinger, A., Massalski, A., and Karsten, U. (2014). Morphology and ultrastructure of *Interfilum* and *Klebsormidium* (Klebsormidiales, Streptophyta) with special reference to cell division and thallus formation. *Eur. J. Phycol.* 49, 395–412. doi: 10.1080/09670262.2014.949308

Morita, R. Y. (1975). Psychrophilic bacteria. *Bacteriol. Rev.* 39, 144–167.

Pushkareva, E., Johansen, J. R., and Elster, J. (2016). A review of the ecology, ecophysiology and biodiversity of microalgae in Arctic soil crusts. *Polar Biol.* 39, 1–14. doi: 10.1007/s00300-016-1902-1905

Rindi, F., Mikhailyuk, T. I., Sluiman, H. J., Friedl, T., and López-Bautista, J. M. (2011). Phylogenetic relationships in interfilum and *Klebsormidium* (Klebsormidiophyceae, Streptophyta). *Mol. Phylogenet. Evol.* 58, 218–231. doi: 10.1016/j.ympev.2010.11.030

Rippin, M., Borchhardt, N., Williams, L., Colesie, C., Jung, P., Büdel, B., et al. (2018). Genus richness of microalgae and Cyanobacteria in biological soil crusts from Svalbard and Livingston Island: morphological versus molecular approaches. *Polar Biol.* 41, 909–923. doi: 10.1007/s00300-018-2252-2

Sabbe, K., Verleyen, E., Hodgson, D. A., Vanhoutte, K., and Vyverman, W. (2003). Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. *Antarct. Sci.* 15, 227–248. doi: 10.1017/S095410200300124X

Škaloud, P., and Rindi, F. (2013). Ecological differentiation of cryptic species within an asexual protist morphospecies: a case study of filamentous green alga *Klebsormidium* (Streptophyta). *J. Eukaryot. Microbiol.* 60, 350–362. doi: 10.1111/jeu.12040

Starr, R. C., and Zeikus, J. A. (1993). UTEX - the culture collection of algae at the University of Texas at Austin 1993 list of cultures. *J. Phycol.* 29, 1–106. doi: 10.1111/j.0022-3646.1993.00001.x

Williams, L., Borchhardt, N., Colesie, C., Baum, C., Komsic-Buchmann, K., Rippin, M., et al. (2016). Biological soil crusts of Arctic Svalbard and of Livingston Island, Antarctica. *Polar Biol.* 40, 399–411. doi: 10.1007/s00300-016-1967-1961

Woelfel, J., Schoknecht, A., Schaub, I., Schaub, I., Enke, N., and Schumann, R. (2014). Growth and photosynthesis characteristics of three benthic diatoms from the brackish southern Baltic Sea in relation to varying environmental conditions. *Phycologia.* 53, 639–651. doi: 10.2216/14-019.1

Yoshitake, S., Uchida, M., Koizumi, H., Kanda, H., and Nakatsubo, T. (2010). Production of biological soil crusts in the early stage of primary succession on a High Arctic glacier foreland. *New Phytol.* 186, 451–460. doi: 10.1111/j.1469-8137.2010.03180.x

Zacher, K., Rautenberger, R., Hanelt, D., Wulff, A., and Wiencke, C. (2009). The abiotic environment of polar marine benthic algae. *Bot. Mar.* 52, 483–490. doi: 10.1515/BOT.2009.082