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Effects of Temperature on Growth and Biochemical Composition of Arctic *Pseudanabaena* sp. and Tropical *Synechococcus* sp.

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ABSTRACT

This study examines the effect of temperature on the growth and biochemical composition of two cyanobacteria: *Pseudanabaena* sp. from the Arctic region and *Synechococcus* sp. from a tropical region. Cyanobacterial isolates were cultivated under three different temperatures: 4±2°C, 15±2°C and 25±2°C. The growth rate of *Pseudanabaena* sp. at 4±2°C, 15±2°C and 25±2°C was 1.61 day^{-1}, 1.62 day^{-1} and 1.53 day^{-1}, while the doubling time was 0.11, 0.18 and 0.08 days, respectively. The growth rate of *Synechococcus* sp. was slightly lower. At 4±2°C, 15±2°C and 25±2°C, the growth rate was recorded at 0.65 day^{-1}, 0.94 day^{-1} and 1.06 day^{-1}, while the doubling time was 0.003, 0.07 and 0.25 days, respectively. Total carbohydrate for *Pseudanabaena* sp. at 4±2°C, 15±2°C and 25±2°C was 207.16±10.03 mg/L, 329.57±189.65 mg/L and 63.32±41.02 mg/L, respectively. At the same temperature, the total carbohydrate for *Synechococcus* sp. was 269.44±81.29 mg/L, 321.15±73.31 mg/L and 1556.84±243.38 mg/L, respectively. It illustrates higher total carbohydrate in *Synechococcus* sp. compared to *Pseudanabaena* sp. At 4±2°C, 15±2°C and 25±2°C, total protein for *Pseudanabaena* sp. was recorded as 5.59±0.09 mg/L, 5.23±0.21 mg/L, and 4.34±0.47 mg/L. Meanwhile, for *Synechococcus* sp., total protein recorded at temperatures 4±2°C, 15±2°C and 25±2°C was 0.47±0.01 mg/L, 0.45±0.01 mg/L and 0.39±0.05 mg/L, respectively. This study shows that the growth rate and biochemical composition of Arctic *Pseudanabaena* sp. and tropical *Synechococcus* sp. were influenced by different temperature levels.

Keywords: Arctic, cyanobacteria, growth, tropical, temperature

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INTRODUCTION

Temperature is an environmental condition that controls the growth and biological chemistry of cyanobacteria, green algae, diatom and others (Gani et al., 2019; Juneja et al., 2013; Morgan-Kiss et al., 2006). Cyanobacteria are prokaryotic, photosynthetic, gram-negative microorganisms that can adapt to environments ranging from low temperatures in the Polar region to high temperatures of more than 80°C in hot springs. They are highly adaptable to a wide range of environmental conditions, including variations in temperature, ultraviolet (UV) irradiance, photo-oxidation, drought and desiccation, nitrogen starvation, heat-cold shocks, anaerobiosis, osmotic and salinity stresses, all of which influence their physiological traits and metabolic activities (Nandagopal et al., 2021; Yadav et al., 2022). Cyanobacteria have evolved exclusive survival strategies to cope with these challenges by producing bioactive compounds that act as protective regulators against external factors. These bioactive metabolites play crucial roles in ensuring the survival of cyanobacteria under diverse environmental conditions (Nandagopal et al., 2021).

Cyanobacteria have various strategies to cope with low temperatures, including the modulation of key enzyme kinetics, the evolution of cold shock and ice-structuring proteins, and the development of liquid biomembranes through the accumulation of polyunsaturated fatty acyl chains (Morgan-Kiss et al., 2006). At low temperatures, cyanobacteria have a dark fixation that decreases the photosynthetic process controlled by enzymes (Tang et al., 1997). Moreover, fatty acid desaturases facilitate the incorporation of polyunsaturated fatty acyl chains into the membrane lipids of cyanobacteria. These enzymes increase the degree of unsaturation in fatty acid chains by adding double bonds at specific positions, forming polyunsaturated fatty acyl chains. Consequently, the buildup of these polyunsaturated fatty acyl chains improves membrane fluidity and helps cyanobacteria sustain cellular activity (Los & Mironov, 2015; Murata & Wada, 1995). This adaptation is important for cyanobacteria to survive in a very harsh environment. Therefore, cyanobacteria is a group of phototrophic microorganisms that can dominate in cold ecosystems, such as the Polar Region, including the Arctic and Antarctic (Vincent, 2007).

Pseudanabaena sp. is a non-heterocystous cyanobacteria belonging to the order Oscillatoriales from the family Pseudanabaenaceae (Acinas et al., 2008; Gao et al., 2018). Simple trichomes characterise this species with a width of less than 4µm. Somehow, the morphology of *Pseudanabaena* sp. is often confused with *Limnothrix* (Meffert, 1987). This species can be found in brackish and freshwater ecosystems and has a strong adaptability and tolerance to various environmental factors such as temperature, low light disturbance and phosphorus deficiency. *Pseudanabaena* sp. is a harmful species, as it often dominates freshwater reservoirs, likely due to its adaptability to these disturbances (Gao et al., 2018). *Synechococcus* sp. is a unicellular cyanobacterium belonging to the order Chroococcales. The natural habitat of *Synechococcus* sp. includes marine and freshwater environments.

This species is one of the major sources of primary production in its habitats and crucial in nutrient cycling, supporting the growth of other marine organisms commonly in the temperate to tropical oceans (Christie-Oleza et al., 2017; Kim et al., 2018; Wang et al., 2011). It has a rod-shaped to coccoid shape less than 3 µm in diameter. *Synechococcus* sp. undergoes binary fission, dividing into equal halves, producing two identical daughter cells in a single plane. This study aims to elucidate the impact of elevated temperature on the growth and biochemical compounds of these two cyanobacteria and compare the response of Arctic and tropical cyanobacteria under different temperature regimes.

MATERIALS AND METHODS

Isolation and Growth Conditions

This study investigated two different regions: the Arctic and the tropical regions. *Pseudanabaena* sp. was isolated from Svalbard Island, Norway (Latitude: 78°N; Longitude: 19.2°E), which represents the polar while *Synechococcus* sp. was isolated from Niah Cave, Malaysia (Latitude: 3.8°N; Longitude: 113.7°E), which represents the tropics. Both isolated species (*Pseudanabaena* sp. and *Synechococcus* sp.) were collected in sterile small containers and transported to the laboratory for further analysis.

Single isolates of *Pseudanabaena* sp. and *Synechococcus* sp. were obtained using streaking and serial dilution methods. Both species were streaked onto BG-11 agar media and maintained in an incubator (Protech, Malaysia) at 15±2°C. The cultures were observed daily to monitor their growth. Serial dilutions were performed several times until pure unialgal strains were obtained. Cultures were grown in BG-11 liquid media. *Pseudanabaena* sp. was incubated at a temperature of 15±2°C; photoperiod of 12L: 12D, with a light intensity of 2000 lux. Meanwhile, *Synechococcus* sp. was grown at 25±2°C, a photoperiod of 12L: 12D, with a light intensity of around 2,000 lux.

Experimental Design

For the experiment, 18 lab flasks (Schott Duran, 250 ml) were filled with 100 ml of BG-11 liquid media. Flasks were divided into two sets: *Pseudanabaena* sp. and *Synechococcus* sp. Each group has three subsets with triplicates that represent 4±2°C, 15±2°C and 25±2°C, respectively. The three temperature ranges (4±2°C, 15±2°C, and 25±2°C) were chosen to represent the native habitats of *Pseudanabaena* sp. (Arctic region) and *Synechococcus* sp. (tropical region). A temperature of 4°C represents the cold conditions of the Arctic, where the *Pseudanabaena* sp. was natively found, 15°C represents a moderate temperature, and 25°C represents the warm conditions of the tropics, where the *Synechococcus* sp. was found. For both species, 10% of its initial inoculum was inoculated into the flask. Each flask was incubated under 4±2°C, 15±2°C and 25±2°C, respectively.

Cyanobacterial Growth Analysis

Cell count was done daily by measuring growth using a Neubauer haemocytometer (MC, China). Before harvesting for carbohydrate and protein analysis, counting was done under a light microscope until the 25th day. The net growth rate of each population was determined using Equation 1:

$$\mu = \ln [Nt/N0]/t \quad [1]$$

where, μ is the population growth rate (d − 1), $N0$ and Nt are initial and final cell densities, and t is the incubation duration in days. The unit for growth rate is day ^{1}.

Equation 1 is used to calculate doubling time, T_g:

$$T_g = \ln 2 / \mu = 0.6931 / \mu \quad [2]$$

Each culture was harvested by centrifugation at 1500 × g for 15 minutes. The supernatant was discarded, and the pellet was freeze-dried to make powder. Protein and carbohydrates were extracted to measure both species' total protein and carbohydrates. Total protein was measured by Bradford's methods (1976), while total carbohydrates were determined by Dubois' methods (Dubois et al., 1956).

Statistical Analysis

Statistical analysis was done using Statistical Package for the Social Sciences (SPSS) software (IBM SPSS Statistic 20). All values represent the mean of triplicate samples for each treatment. Error bars in the figures illustrate the standard deviations of these triplicates. Significant differences ($p < 0.05$) between values were determined using two-way Analysis of Variance (ANOVA) and Duncan's Post Hoc Test to identify which specific group means are significantly different.

RESULTS

Biomass Productivity

For 25 days, *Pseudanabaena* sp. and *Synechococcus* sp. biomass productivity was evaluated at various temperatures. Two-way ANOVA, between-groups analysis of variance, was conducted to explore the impact of different temperatures on growth and biochemical compounds. The highest growth rate achieved for *Pseudanabaena* sp. was at 15±2°C (1.62 day^{-1}) (Table 1, Figure 1) with the highest doubling time of 0.18 day (Table 1, Figure 2). At 4±2°C, *Pseudanabaena* sp. showed a growth rate of 1.61 day^{-1} (Figure 1) and a doubling time of 0.11 day (Figure 2), which is almost adjacent to the readings at 15±2°C. Post-hoc comparisons using the Duncan Test indicated that the growth rate and doubling time for *Pseudanabaena* sp. at three diverse temperatures were nearly identical ($p > 0.05$) (Table

1). For *Synechococcus* sp., the maximum growth rate was observed at 25±2°C (1.06 day^{-1}) (Table 1, Figure 1), and the highest doubling time was recorded at 0.25 day^{-1} (Table 1, Figure 2). The lowest growth rate for *Synechococcus* sp. was at 4±2°C, while the lowest doubling time was determined at 0.003 day^{-1}. Duncan Test showed that the same growth rate for three temperatures was significant ($p > 0.05$), while the doubling time for 25±2°C was significantly different from other temperatures ($p < 0.05$).

Table 1
Functional growth performance parameters for Pseudanabaena *sp. and* Synechococcus *sp. cells grown under three different temperatures*

Isolates and growth		Temperature (°C)		
		4	15	25
Pseudanabaena sp.	Growth rate (day^{-1})	1.61±0.60^{b}	1.62±0.08^{b}	1.50±0.70^{a,b}
	Doubling time (day)	0.11±0.02^{a,b}	0.18±0.04^{b,c}	0.08±0.06^{a,b}
Synechococcus sp.	Growth rate (day^{-1})	0.63±0.12^{a}	0.95±0.80^{a,b}	1.06±0.05^{a,b}
	Doubling time (day)	0.003±0.001^{a}	0.070±0.015^{a,b}	0.250±0.090^{c}

Note. Values given are the means with a standard deviation of measurements on triplicate cultures. Different superscript letters indicate significant differences in values ($p < 0.05$)

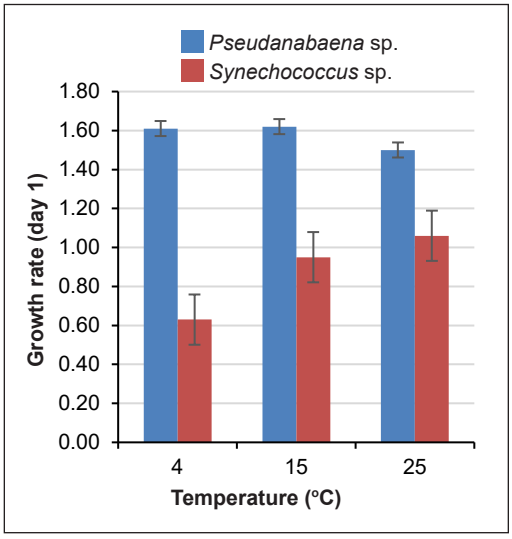

Figure 1. The growth rate of *Pseudanabaena* sp. and *Synechococcus* sp. at different temperature regimes (mean growth rate ± standard deviation)

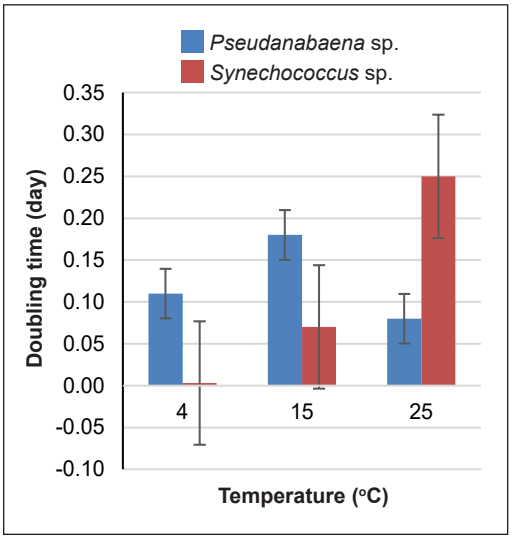

Figure 2. Doubling time of *Pseudanabaena* sp. and *Synechococcus* sp. at different temperature regimes (mean doubling time ± standard deviation)

Total Carbohydrate and Total Protein

Table 2 illustrates the total carbohydrates for *Pseudanabaena* sp. and *Synechococcus* sp. at different temperatures. For *Pseudanabaena* sp., the highest total carbohydrate was recorded at 15±2°C (329.57±189.65 mg/L), while the lowest total carbohydrate was recorded

at 25±2°C (63.32±41.02 mg/L). For *Synechococcus* sp., the highest total carbohydrate was recorded at 25±2°C (1556.84±243.38 mg/L), while the lowest total carbohydrate was recorded at 4±2°C (269.44±81.29 mg/L). Post-hoc Duncan Test (Table 2) showed that total carbohydrates for *Pseudanabaena* sp. were not significant ($p > 0.05$), whereas total carbohydrates for *Synechococcus* sp. at 25±2°C were dramatically higher than other temperatures ($p = 0.001$). Figure 4 examined the total protein for *Pseudanabaena* sp. and *Synechococcus* sp. *Pseudanabaena* sp. recorded higher total protein than *Synechococcus* sp. The total protein for *Pseudanabaena* sp. and *Synechococcus* sp. was highest at 4±2°C when compared to 15±2°C and 25±2°C ($p < 0.05$). The total protein of both cyanobacteria showed the same prototype- total protein declined as the temperature increased.

Table 2
Functional biochemical growth parameters for Pseudanabaena *sp. and* Synechococcus *sp. cells grown under three different temperatures*

Isolates and biochemical components		Temperature (°C)		
		4	15	25
Pseudanabaena sp.	Carbohydrates (mg/L)	252.35±52.35^{a,b}	329.57±189.65^{b}	63.32±41.02^{a}
	Protein (mg/L)	5.6±0.008^{f}	5.2±0.060^{e}	4.5±0.040^{d}
Synechococcus sp.	Carbohydrates (mg/L)	269.44±81.29^{a,b}	322.45±75.26^{a,b}	1556.84±243.38^{c}
	Protein (mg/L)	0.4±0.010^{c}	0.3±0.011^{b}	0.2±0.006^{a}

Note. Values given are the means with standard deviations of measurements on triplicatecultures. Different superscript letters indicate significant differences in values ($p < 0.05$)

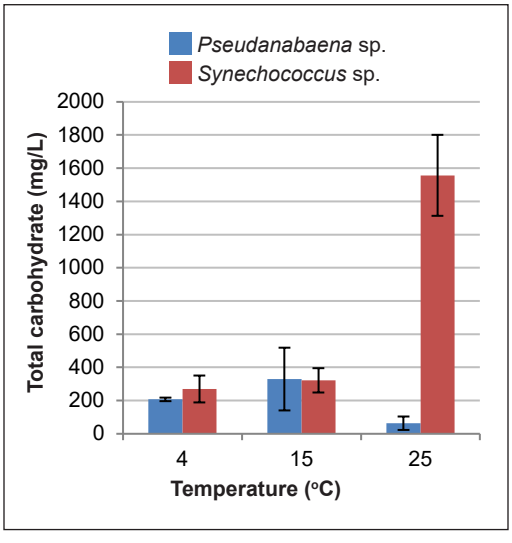

Figure 3. Total carbohydrate of *Pseudanabaena* sp. and *Synechococcus* sp. at different temperature regimes (mean total carbohydrates ± standard deviation)

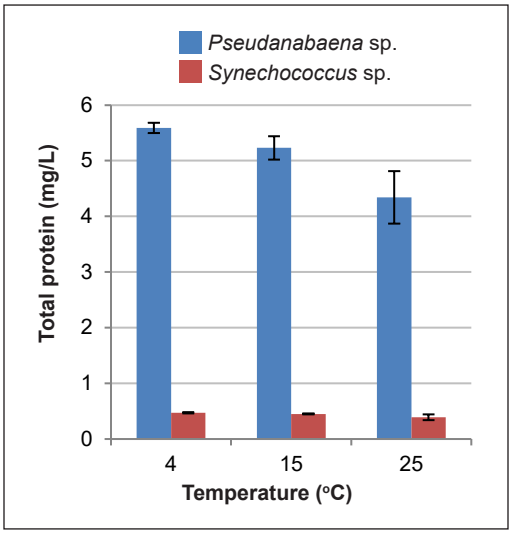

Figure 4. Total protein of *Pseudanabaena* sp. and *Synechococcus* sp. at different temperature regimes (mean total protein ± standard deviation)

DISCUSSION

One of the aims of this investigation is to determine if temperature acts as a controlling factor for cyanobacteria growth. In some cases, *Pseudanabaena* sp. responded better to experimental conditions with different temperatures than *Synechococcus* sp. (Gao et al., 2018). However, temperature did have a marked effect on *Synechococcus* sp. growth rate. Cell division rates for *Pseudanabaena* sp. remained unaffected by the experimental temperature changes. Based on Figure 1, we can conclude that the *Pseudanabaena* sp. is a psychrotolerant or psychrotrophic species. According to Moyer and Morita (2007), psychrotolerant or psychrotrophic is a species of organism from a cold environment that can adapt to temperatures higher than the ambient temperature of 15°C. However, Figures 1 and 2 also illustrated that *Pseudanabaena* sp. had the lowest growth rate and doubling time as temperature increased. This result is the same as recorded by Tang et al. (1997), where the growth of psychrotrophic species will decrease as temperature increases.

Additionally, previous studies have demonstrated that the Antarctic and Arctic strains of the genus *Pseudanabaena* are psychrotolerant, exhibiting optimal growth temperatures ranging from 8°C to 15°C; they are also able to grow and develop at temperatures exceeding 20°C (Averina et al., 2020; Khan et al., 2017). It may be due to thermal instability and denaturation of molecular compounds in the cyanobacteria. At higher temperatures, proteins and nucleic acids lose the basic conformational structure in their native state, leading to cell activity disruption and probably cell death. The sudden growth from day 0 to day 3 was because of the exponential accumulation of cyanobacteria biomass in stock culture (Tang et al., 1997) due to the change in temperature from 15°C to 4°C. Experiment results indicated that temperature above 15°C limits the growth of *Pseudanabaena* sp.

Figure 1 shows that as the temperature increases, the growth rate of *Synechococcus* sp. increases. Figure 2 demonstrated a similar pattern, with doubling time directly proportional to temperature. A previous study by Prihantini et al. (2016) also observed that *Synechococcus* strains achieved their highest cell densities and optimal growth temperatures between 30°C and 35°C, indicating that an increase in temperature within this range can enhance their growth due to the increase of metabolic rate in algae that can enhance the activity of the species. The enzyme that catalyses the biochemical reaction rate depends on temperature changes (Sakamoto et al., 1998). According to Beardall and Raven (2004), temperature will increase the reaction rate of Ribulose-1, 5-bisphosphate carboxylase oxygenase (RUBISCO) and enhance the growth rate of cyanobacteria, given that inorganic carbon or other factors do not limit the growth. Tropical *Synechococcus* sp. showed the lowest growth at 4ºC as protein is less stable and is difficult to synthesise at low temperatures (Sanfelice & Temussi, 2016). It is another mechanism that can limit growth at low temperatures. Some research suggested that low temperature decreases the rate of nutrient uptake from the environment, which could be the rate-limiting step for the growth of microorganisms (Nedwell & Rutter, 1994).

As shown in Figure 3, the total carbohydrate for *Synechococcus* sp. at 25±2°C was higher than *Pseudanabaena* sp. because carbohydrate accumulates in cyanobacterial cells due to osmotic reactions (Warr et al., 1985). The accumulation of carbohydrates keeps water in the cell, which protects it from dehydration. Because *Synechococcus* sp. was isolated from Niah Cave, the existence of light might affect the accumulation of carbohydrates. It might stress this species as its natural environment is dark. Thus, the production of carbohydrates is part of the defence in response to stress conditions (De Philippis & Vincenzini, 1998; Otero & Vincenzini, 2003; Trabelsi et al., 2009; Wingender et al., 1999). Khajepour et al. (2015) reported that *Nostoc calcicola* shows high carbohydrate and carotenoid content when light intensity increases. Besides temperature, salinity also occurs in the accumulation of carbohydrates in cyanobacteria because of the osmotic reaction that prevents dehydration (Hershkovitz et al., 1991; Reed & Stewart, 1985). The form of mucopolysaccharides or exopolymeric substances (EPS) can make the liquid water flow slowly when freezing up and thawing. In addition, the EPS may force ice crystal formation to create well away from cyanobacterial cells (Vincent, 2007). It is also shown in *Nostoc commune*, where EPS protects cyanobacterium from desiccation and freezing up (Tamaru et al., 2005; Vincent, 2007). Increased production of EPS and sucrose in the algal cells protects them from osmotic damage by maintaining the cellular osmotic equilibrium between the intracellular and extracellular environment (Chen et al., 2006).

To tolerate stress conditions, protein profiling and newly forming proteins can help cyanobacteria survive (Weber & Jung, 2002). In Figure 4, the total protein for *Pseudanabaena* sp. was higher than *Synechococcus* sp. in all degrees of temperature. *Pseudanabaena* sp. was isolated from the Arctic region since there was a change in temperature from 15°C (stock culture) to 4°C. This species can have high total protein because the accumulation of proteins such as dehydrins might be how Arctic cyanobacteria adapt to survive in cold environments (Dasauni et al., 2021). This adaptation is known as cyano-dehydrins. During osmotic adaptation, the protein acts as a regulator that prevents osmotic stress due to the adaptation in a cold environment that operates within desiccation–tolerant in cyanobacterial cells (Close & Lammers, 1993). Thus, Arctic cyanobacteria can have higher total protein than tropic cyanobacteria. At low temperatures, membrane lipid unsaturation increases (Zheng et al., 2011), and this can be considered an acclimatised response to balance the decreased functionality of biological membranes at low temperatures by increasing the membrane fluidity for cellular viability under temperature stress. Its increase in membrane lipid unsaturation is a conserved adaptation response that allows cells to maintain the appropriate fluidity of membrane lipid bilayers, ensuring cell viability under temperature stress (Uemura et al., 2005). The susceptibility of a protein to high-temperature degradative reactions

seems to be dependent on the conformational integrity of the protein at that particular temperature (Daniel et al., 1996). Figure 4 also shows that protein content decreased as the temperature increased. Temperature affects phytoplankton growth, especially when enzyme kinetics are controlled.

In response to low temperatures, an increase in protein content prompts the production of enzymes to prevent the loss of membrane fluidity, highlighting the essential role of generating cold-active enzymes in microalgae to maintain cellular functions and ensure survival under low-temperature stress conditions (Gao et al., 2023; Georlette et al., 2004). This pattern of the graph (Figure 4) was similar to some marine microalgae such as *Pavlova lutheri, Skeletonema costatum* and also *Euglena gracilis* (Carvalho et al., 2009; Cook, 1963; Falkowski, 1977).

CONCLUSION

This research concludes that *Pseudanabaena* sp. and *Synechococcus* sp. showed higher responses at their ambient temperature. This finding suggested that cyanobacteria are highly adaptive to their native environment but can survive in extreme conditions. This adaptive nature is based on the mechanism that allows its adaptation, the rate of adaptation, the cost of fitness, the growth rate, and the photosynthetic efficiency of this adaptation. *Pseudanabaena* sp. from the Arctic region is a psychrotrophic species. The growth pattern of this species indicates that, after reaching the optimum temperature, the growth of cold-tolerant cyanobacteria decreases with rising temperatures. For future research, this study will consider the employment and comparison of cyanobacteria from polar and tropic regions for biofuel production. Biofuel is the most promising solution for global energy calamity and climate change.

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