



# Nutrient limitation of microbial phototrophs on a debris-covered glacier



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## ABSTRACT

Photosynthetic microbial communities are important to the functioning of early successional ecosystems, but we know very little about the factors that limit the growth of these communities, especially in remote glacial and periglacial environments. The goal of the present study was to gain insight into the degree to which nutrients limit the growth of photosynthetic microbes in sediments from the surface of the Toklat Glacier in central Alaska. Previous studies and historical observations indicated that this environment is dominated by unique soil algae, and that succession from a microbial to a plant-dominated system is very slow. We used a soil microcosm approach to determine if nitrogen (N) and/or phosphorus (P) additions would affect the development and final biomass of microbial phototroph communities in this system. We found that fertilization with P significantly increased the exponential growth rate ( $r$ ), but P alone did not affect the final percent soil cover ( $K$ ) by microbial phototrophs. Nitrogen alone had no effect on either  $r$  or  $K$ , but the combination of P and N dramatically increased  $K$ , thus showing that algal growth rate in this system is likely P-limited, but total productivity may be co-limited by P and N. In addition, nutrient treatments differentially stimulated microbial groups resulting in significantly different microbial communities among treatments. Overall, these results give a preliminary indication of the factors that might limit the development and productivity of photosynthetic microbial communities in an extreme and remote glacial system.

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## 1. Introduction

Very few studies have examined nutrient limitation of photosynthetic community development in plant-free periglacial and glacial environments (Schmidt et al., 2012). The development of photosynthetic microbial communities is a critical early step in primary succession, contributing to soil formation that in turn is necessary for the establishment of macroscopic plant communities (Belnap and Lange, 2001, Nemergut et al., 2007). Schmidt et al. (2012) observed that in the glacial forelands of the Puca glacier in Perú, the development of photosynthetic crust communities was limited by phosphorus availability. However, this limitation may or may not be exclusive to that site or to the Peruvian Andes. Other environments in the cryosphere may impose different limitations on the development of microbial phototroph communities,

especially since cold desert environments differ in important biogeochemical factors (Schmidt et al., 2011a).

One type of cold desert environment that has received very little study are debris-covered glaciers, which are very common and extensive in terms of geographic coverage, especially in active geological areas such as the Himalayas and Alaska Range (Nakawo et al., 2000; Scherler et al., 2011). This environment is characterized by a thin layer of mineral debris on top of glacial ice, which is deposited allocthonously from the glacier's surroundings. One such glacier is the Middle Fork Toklat Glacier in the Alaskan interior (Alaska Range) which is covered with oligotrophic mineral soils, is not colonized by plants (Schmidt and Darcy, 2014), and is located in Denali National Park and Preserve, which has very low rates of nitrogen deposition (Fenn et al., 2003). Before the present study, no work had been done on microbial phototrophs and nutrient limitation in the extreme environment atop debris-covered glaciers. However, nutrient limitation has been observed in heterotrophic microbial communities in several early-succession cold desert biomes. P limitation was observed for heterotrophic microbes of periglacial soils in the Colorado Rocky Mountains (King et al., 2008) and Peruvian Andes (Schmidt et al., 2011b), while N limitation

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(after C limitation was alleviated) was observed in the Swiss Alps (Göransson et al., 2011). However, nutrient limitations of heterotrophic communities may not translate to their co-occurring phototroph communities since microbial phototrophs may have access to different pools of P than their heterotrophic counterparts (Cleveland and Liptzin, 2007).

Although there has been much previous work on nutrient limitation and microbiology of cold-desert environments (King et al., 2008; Göransson et al., 2011; Schmidt et al., 2011b, 2012; Knelman et al., 2014), most of it has focused on recently deglaciated landscapes. However, except for the current study, work on supraglacial nutrient limitation has been limited to cryoconite holes (Stibal et al., 2009), which are substantially different from the soil-like surface of the Toklat Glacier. Cryoconite holes form when small amounts of debris are warmed by solar radiation and melt into the ice forming enclosed micro-communities. Although this process may happen in places atop the Toklat glacier, the supraglacial debris layer is over 20 cm thick, enough so that the ice beneath the debris cannot be seen. Microbiological studies of supraglacial debris are rare, with only two studies focusing on bacteria atop debris-covered glaciers (Darcy et al., 2011; Franzetti et al., 2013). Unsurprisingly, culture-independent studies of microscopic eukaryotes in supraglacial debris are even rarer yet, with the only currently published work being our previous study of unique algal clades on the Toklat Glacier (Schmidt and Darcy, 2014).

Here, we use a microcosm experiment, biogeochemical analysis, and culture-independent molecular methods to better understand the extreme supraglacial environment, and the role nutrient limitation may play in limiting microbial growth on top of a debris-covered glacier. To measure nutrient limitation, we employed and improved upon recently developed microcosm-based experimental protocols for comparing the degree to which common limiting nutrients (N and P) influence the growth of diminutive photosynthetic communities (Schmidt et al., 2012). We have taken this approach a step farther by phylogenetically characterizing the microbial communities from these microcosms to better understand selection processes that occur under different nutrient limitation conditions, and how they relate to organisms that may be found *in situ*. Together, our results form a detailed glimpse of phototrophic life in this harsh environment, and provide new insights into how different cryospheric bacteria and microbial eukaryotes may be affected by nutrient limitation.

## 2. Methods

### 2.1. Nutrient addition experiment

Microcosm plates were created using homogenized soil samples collected from atop the Toklat Glacier by Darcy et al. (2011). Homogenization was used to ensure that starting communities were similar among microcosms, and also representative of the organisms found *in situ*. A total of 20 microcosms were made, each consisting of 13 g of soil added to a 55 mm diameter Petri dish (Fisher Scientific 8-757-13A), sealed with Parafilm (Pechiney Plastic Packaging, Menasha WI, USA). Treatments consisted of a control (no nutrient addition), +N, +P, and +N+P. For each treatment, 75  $\mu\text{g}$  of N (as  $\text{NH}_4\text{NO}_3$ ), P (as  $\text{KH}_2\text{PO}_4$ ), or both were added (in aqueous solution) per gram of soil. All soils were initially amended to 70% of water holding capacity as described elsewhere (Schmidt et al., 2011b, 2012). Water holding capacity averaged 29% of dry weight across microcosms, therefore aqueous concentration was approximately 370  $\mu\text{g}$  of N and/or P per ml of water. Preliminary experiments indicated that these concentrations were high enough to overcome nutrient limitations in calcareous, early successional soils (Schmidt et al., 2011b, 2012). Microcosms were incubated at

21 °C under 16 h of light per 24 h, conditions that approximately mimic the relatively mild summer conditions at the toe of the Toklat Glacier (unpublished data). The arrangement of the plates was randomized every three days to account for any variation in light and temperature. Microcosms were surveyed twice weekly for coverage of microbial phototrophs using the field of view (FOV) method described by Schmidt et al. (2012), for a total of 15 time points over 51 days. When FOV measurements began to saturate (plateau), a variation of the point-intercept method was used instead, where a reticule was placed on the microscope's objective. Instead of counting a 'hit' when a photosynthetic colony was within the field of view, a 'hit' was counted when the cross-hairs (a single point) of the reticule intersected any photosynthetic organism or structure. This method was much more time consuming, but allowed for more accurate estimates of percent cover. Both types of measurement (FOV and point-intercept) were used in conjunction for several measurement periods before the FOV measurements began to reach saturation at day 34.

### 2.2. In-silico methodological validation

To correlate the two methods, an *in-silico* microcosm experiment was run (R code available upon request), which used both the FOV and point-intercept methods on randomly generated microcosm plates. To ensure a broad distribution of covers across generated microcosm plates, plates were generated with preset naïve covers ranging from 0 to 80% cover, calculated by the total area of all colonies divided by the total area of the plate. This naïve cover is inaccurate by design because of overlap between colonies, however it was only used to ensure a wide range of actual *in silico* covers (as estimated by percent cover) for correlative purposes. We also confirmed that the *in-silico* point-intercept method is highly accurate, by using Adobe Photoshop's (Adobe Inc., San Jose CA, USA) magic wand tool to calculate the ratio of green pixels to white pixels on graphical representations of the *in-silico* microcosms (Supplemental Fig. 1, first panel). The trend between FOV and point-intercept data observed in the *in-silico* experiment was best modeled using a general 1-parameter exponential decay model (Equation (1)) (Supplemental Fig. 1, second panel), which was fit to the observed data using the Gauss-Newton algorithm in R 3.0.2 (R Core Team, 2013) (Supplemental Fig. 1, third panel). This model was then used to convert real FOV data from before day 34 of the microcosm experiment to percent cover estimates.

Equation (1): Exponential decay.

$$f(x) = 1 - e^{-Ax} \quad (1)$$

### 2.3. Growth curve modeling and statistical analysis

Time series of percent cover data for each of the 20 microcosms were modeled using the general logistic growth function (Equation (2)) in R using the Gauss-Newton algorithm. The logistic growth function we used has been described elsewhere (e.g. Schmidt et al., 2011b) and models growth as a function of time ( $t$ , days), with three parameters: The upper asymptote ( $K$ , final percent cover), the exponential growth rate ( $r$ ,  $\text{days}^{-1}$ ), and the position of the inflection point ( $i$ , days). The point on the logistic curve where  $t = i$  has the steepest instantaneous growth rate (i.e. % cover gained per day). In this version of the logistic equation, the lower asymptote is fixed at zero. Fit parameter values for each nonlinear model were used in three 2-way ANOVAs with interaction to test for the effects of N and P addition on growth response, using Boolean independent variables for N and P.

Equation (2): Logistic growth.

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