Inorganic carbon addition stimulates snow algae primary productivity

Trinity L. Hamilton[1,*], Jeff R. Havig[2]

Author 1: Hamilton T (trinity.hamilton@uc.edu)

Author 2: Havig J (jeffhavig@gmail.com)

[1] Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221, USA

[2] Department of Geology, University of Cincinnati, Cincinnati, OH 45221, USA

*correspondence:

Trinity L Hamilton. 731F Rieveschl Hall, Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221, USA. Phone: +15135569700, Fax: +5135565299, Email: trinity.hamilton@uc.edu.

Running title: Snow algae are inorganic-carbon limited

Keywords: snow algae, inorganic carbon, glacier, primary productivity, CO_2, photosynthesis, Neoproterozoic, albedo

SUMMARY

Earth has experienced glacial/interglacial oscillations accompanied by changes in atmospheric CO_2 throughout much of its history. Today over 15 million square kilometers of Earth's land surface is covered in ice including glaciers, ice caps, and the ice sheets. Glaciers are teeming with life and supraglacial snow and ice surfaces are often darkened by the presence of photoautotrophic snow algae, resulting in accelerated melt due to lowered albedo. Few studies report the productivity of snow algae communities and the parameters which constrain their growth on supraglacial surfaces—key factors for quantifying biologically induced albedo effects (bio-albedo). We demonstrate snow algae primary productivity is stimulated by the addition of inorganic carbon. Our results indicate a positive feedback between increasing CO_2 and snow algal primary productivity, underscoring the need for robust climate models of past and present glacial/interglacial oscillations to include feedbacks between supraglacial primary productivity, albedo, and atmospheric CO_2.

MAIN BODY

Earth has experienced intervals of glacial and interglacial periods in its history including Snowball Earth events (Hoffman *et al*., 1998; Rasmussen *et al*., 2013). Today, glaciers and ice sheets are integral to Earth's climate and hydrological system—they influence regional and global climate, are sensitive to climate change, and are the largest freshwater reservoir on Earth (Clark *et al*., 1999; Edwards *et al*., 2014). Geologic and geochemical evidence suggest glacial/interglacial oscillations are coincident with lower atmospheric CO_2 (Sigman and Boyle, 2000) and exacerbated by lower solar luminosity (Gough, 1981). For instance, models indicate overcoming high planetary albedo during Snowball Earth events required greenhouse warming caused by the accumulation of high levels of CO_2 from volcanic outgassing accompanied by decreases in silicate weathering (Caldeira and Kasting, 1992; Allen and Etienne, 2008). Due to human activity, atmospheric CO_2 is now above 400 ppm (Waters *et al*., 2016) and from 1999 to 2010, CO_2 was emitted at a rate 100 times as fast as during the last glacial termination (Wolff, 1999). Coincident with increasing CO_2, average global temperatures have increased (~1°C over the past century) leading to glacial retreat and receding snowpack.

Glaciers and ice sheets are host to diverse ecosystems including supraglacial communities that contribute to local and global biogeochemical cycles (Anesio *et al*., 2012). Snow algae (eukaryotic photoautotrophs) are key primary producers on supraglacial habitats in the Arctic and on glaciers and snowfields throughout the world where they thrive in high-irradiation environments (Morgan-Kiss *et al*., 2006; Boetius *et al*., 2015). To overcome this high irradiance, snow algae produce secondary carotenoids resulting in blooms of red algal biomass (Remias *et al*., 2005), which darkens snow and ice surfaces. In Sierra Nevada snowfields, snow algae abundance was negatively correlated to surface albedo (Thomas and Duval, 1995). Similarly, in the Arctic, red algal blooms darken the snow/ice surface lowering surface albedo by as much as 13% over the melt season (Lutz *et al*., 2016) and increasing melt rates (Musilova *et al*., 2016; Cook *et al*., 2017).

Allochthonous material delivered to snow and ice surfaces such as forest fire-derived black carbon, Saharan or pro-glacial mineral dust, volcanic ash, and anthropogenic pollution causes increased absorption of solar radiation and locally accelerated melting. These effects can be far reaching—a darkening of the Greenland ice sheet has been observed coincident with increased melt (Tedesco *et al*., 2016). While the effects of inorganic material on albedo have been quantified, climate models have not traditionally accounted for melting caused by snow algae (Lutz *et al*., 2016). These efforts are complicated by the difficulty in separating abiotic albedo from biologically induced darkening, or bio-albedo, as well as a paucity of data on snow algae distribution and density. However, a recently developed spectral model for bio-albedo indicates algal blooms can influence snowpack albedo and melt rate (Cook *et al*., 2017). The model indicated algae biomass has a greater effect than pigment concentration, suggesting a positive correlation between supraglacial algal blooms and accelerated melt.

Understanding both geologic glacial/interglacial oscillations and predicting future climate requires integrating climate models, carbon cycling, and planetary albedo. Algal clades, including green algae, evolved prior to Neoproterozoic glaciations (Knoll, 1992). Thus, the cosmopolitan nature of snow algae and their widespread distribution on snowpacks worldwide (Hisakawa *et al*., 2015) facilitates their inclusion in these models across space and time. Snow algae are now recognized as a key component driving melting yet the role of increasing CO_2 on snow algae primary productivity (a proxy for growth), and thus albedo, remains unconstrained. Here we examined community composition and primary productivity (carbon fixation rates) of snow algae communities on supraglacial snowfields on glaciers on stratovolcanoes in the Pacific Northwest. We targeted Gotchen Glacier on Mt. Adams, Eliot Glacier on Mt. Hood, and Collier Glacier on North Sister (Fig. 1; Table S1) where our previous data suggested photoautotrophic snow algae could be inorganic carbon-limited (Hamilton and Havig, 2017).

Stratovolcano supraglacial microbial community composition

Snow algae assemblages were comprised predominantly of eukaryotic 18S rRNA gene sequences affiliated with C*hlamydomonas* spp. and *Chloromonas* spp. within the *Chlorophyta* (green algae)(Fig. 1). OTUs affiliated with strains of C*hlamydomonas nivalis* were abundant in supraglacial snow from Gotchen and Eliot Glaciers whereas OTUs affiliated with a *Chloromonas* spp. were the most abundant in the Collier Glacier snow sample. The sequences recovered are similar to those recovered from the Arctic, further indicating snow algae are cosmopolitan (Lutz *et al*., 2016). Bacterial OTUs most closely related to *Chitinophagaceae*, *Cytophagaceae*, and *Sphingobacteriaceae* were abundant in snow algae samples from the three glaciers (Fig. 1). The recovery of these bacteria is consistent with previous studies of supraglacial snow (Boetius *et al.*, 2015; Lutz *et al.*, 2016; Hamilton and Havig, 2017) and highlights a role for these populations in degradation of complex organic carbon on the glacial surface.

Stratovolcano snow algae primary productivity

Carbon fixation rates were examined in a series of microcosms in supraglacial snow over a range of dissolved inorganic carbon (DIC) concentrations (50 µM to 1 mM $NaH^{13}CO_3$) where natural DIC concentration in snow samples ranged from 9 to 23 µM. At all sites, an increase in light-dependent carbon fixation was observed with increasing concentration of (DIC) concentration (Fig. 2). In microcosms amended with 50 µM $NaH^{13}CO_3$ (Fig. 2; Table S1), rates of carbon assimilation ranged from ~17 µg C/g $C_{biomass}$/hr in supraglacial snow algae from Eliot Glacier to ~42 µg C/g $C_{biomass}$/hr at Collier Glacier. Microcosms amended with 500 µM or 1 mM $NaH^{13}CO_3$ incorporated significantly more carbon than assays amended with 50 µM or 100 µM $NaH^{13}CO_3$ (Fig. 2; Table 1). This effect was particularly pronounced at Eliot and Gotchen Glaciers where rates increased 77-108% in the presence of elevated $NaH^{13}CO_3$ (50 µM vs. 1 mM). The increase in carbon assimilation rates at Collier Glacier between 50-100 µM $NaH^{13}CO_3$ and 500 to 1mm µM $NaH^{13}CO_3$ was ~20-25%.

Implications for future and past climate models

Our data indicate snow algae primary productivity is stimulated by the addition of CO_2. Assuming carbon fixation is a proxy for growth, increased primary productivity would be correlated with lower albedo and increased melt. This positive feedback suggests increasing atmospheric CO_2 concentration will drive increased primary productivity, accelerating glacial retreat, especially for mountain glaciers that are particularly susceptible to climate change. Our data support recent interest in quantifying the effects of bio-albedo and underscore the need for integrating algal–albedo interactions and variable (increasing) CO_2 in models aimed at interpreting Earth’s past glacial/interglacial oscillations as well as current and future climate models.

ACKNOWLEDGEMENTS

We thank J. Miller and H. Roger for technical assistance in the field. We are particularly grateful to J. Miller. We thank the National Forest Service for facilitating access to the sample locations. We also thank B. Havig and S. Havig for their generosity in letting us use their home as a base of operations and their garage as a field laboratory. We are also grateful to A. Diefendorf for access to and use of the Stable Isotope Geochemistry Lab in the Department of Geology at the University of Cincinnati and C. Motley for assistance with processing samples. This research was supported by funds from the University of Cincinnati LEAF program and from the University of Cincinnati.

AUTHOR CONTRIBUTIONS

T.L.H. and J.R.H. designed the study, performed the field work, and completed all analyses. T.L.H. wrote the manuscript with substantial input from J.R.H.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

FIGURE LEGENDS

Figure 1. Map of sampling site locations and composition of small subunit 16S and 18S rRNA gene sequences. OTUs for each library were binned at the Family level.

Figure 2. Box-Whisker plots of carbon assimilation rates by supraglacial communities. The horizontal line in each box indicates the median and closed circles represent the mean (n=3 for each treatment). Dark treatments were amended with 100 µM $NaH^{13}CO_3$.

REFERENCES

Allen PA, Etienne JL. (2008). Sedimentary challenge to Snowball Earth. *Nat. Geosci.* **1**, 817-825. (doi:10.1038/ngeo355)

Anesio AM, Laybourn-Parry J. (2012). Glaciers and ice sheets as a biome. *Trends Ecol. Evolut.* **27**, 219-225. (doi:10.1016/j.tree.2011.09.012)

Boetius A, Anesio AM, Deming JW, Mikucki JA, Rapp JZ. (2015). Microbial ecology of the cryosphere: sea ice and glacial habitats. **13**, 677-690. (doi:10.1038/nrmicro3522)

Caldeira K, Kasting JF. (1992). Susceptibility of the early Earth to irreversible glaciation caused by carbon dioxide clouds. *Nature* **359**, 226-228. (doi:10.1038/359226a0)

Clark PU, Alley RB, Pollard D. (1999). Northern Hemisphere Ice-Sheet Influences on Global Climate Change. *Science* **286**, 1104-1111. (doi:10.1126/science.286.5442.1104)

Cook JM, Hodson AJ, Taggart AJ, Mernild SH, Tranter, M. (2017). A predictive model for the spectral "bioalbedo" of snow. *J. Geophys. Res. Earth Surf.* **122**, 434–454. (doi:10.1002/ 2016JF003932)

Edwards A, Irvine-Fynn T, Mitchell AC, Rassner SME. (2014). A germ theory for glacial systems? *Wiley Interdiscip. Rev. Water* **1**, 331–340. (doi:10.1002/wat2.1029)

Gough DO. (1981). Solar interior structure and luminosity variations. *Sol. Phys.,* **74**, 21–34.

Hisakawa N, Quistad SD, Hester ER, Martynova D, Muaghan H, Sala E *et al*. (2015). Metagenomic and satellite analyses of red snow in the Russian Arctic. Peer J, **3**:e1491. (doi:10.7717/peerj.1491)

Hoffman PF, Kaufman AJ, Halverson GP, Schrag DP. (1998). A Neoproterozoic snowball earth. *Science* **281**, 1342-1346. (doi:10.1126/science.281.5381.1342)

Knoll AH. (1992). The Early Evolution of Eukaryotes: A Geological Perspective. *Science* **256**, 622-627. (doi:10.1126/science.1585174)

Lutz S, Anesio A, Raiswell R, Edwards A, Newton RJ, Gill F *et al*. (2016). The biogeography of red snow microbiomes and their role in melting arctic glaciers. *Nat. Commun.* **7**:11968. (11968, doi:10.1038/ncomms11968)

Morgan-Kiss RM, Priscu JC, Pocock T, Gudynaite-Savitch L, Huner NPA. (2006). Adaptation and Acclimation of Photosynthetic Microorganisms of Permanently Cold Environments. *Microbiol. Mol. Biol. Rev.* **70**, 222-252. (doi:10.1128/MMBR.70.1.222-252.2006)

Musilova M, Tranter M, Bamber JL, Takeuchi N, Anesio AM. (2016). Experimental evidence that microbial activity lowers the albedo of glaciers. *Geochem. Perspect. Lett.* **2**, 106–116. (doi:10.7185/geochemlet.1611)

Rasmussen B, Bekker A, Fletcher IR. (2013). Correlation of Paleoproterozoic glaciations based on U–Pb zircon ages for tuff beds in the Transvaal and Huronian Supergroups. *Earth Planet. Sci. Lett.* **382**, 173-180. (doi:10.1016/j.epsl.2013.08.037)

Remias D, Lütz-Meindl U, Lütz C. (2005). Photosynthesis, pigments and ultrastructure of the alpine snow alga *Chlamydomonas nivalis*. *Eur. J. Phycol.* **40**, 259–268. (doi;10.1080/09670260500202148)

Sigman DM, Boyle EA. (2000). Glacial/interglacial variations in atmospheric carbon dioxide. *Nature* **407**, 859-869. (doi:10.1038/35038000)

Tedesco M, Doherty S, Fettweis, X, Alexander P, Jeyaratnam J, Stroeve J. (2016). The darkening of the Greenland ice sheet: trends, drivers, and projections (1981-2100). *Cryosph*. **10**, 477–496. (doi:10.5194/tc-10-477-2016)

Waters CN, Zalasiewicz J, Summerhayes C, Barnosky AD, Poirer C, Gałuszka A *et al*. (2016). The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science* **351**, aad2622. (doi:10.1126/science.aad2622)

Wolff EW. (2011). Greenhouse gases in the Earth system: A palaeoclimate perspective. *Philos. Trans. R. Soc. London Ser. A* **369**, 2133–2147. (doi:10.1098/rsta.2010.0225pmid:21502180)

Figure 1. Map of sampling site locations and composition of small subunit 16S and 18S rRNA gene sequences. OTUs for each library were binned at the Family level.

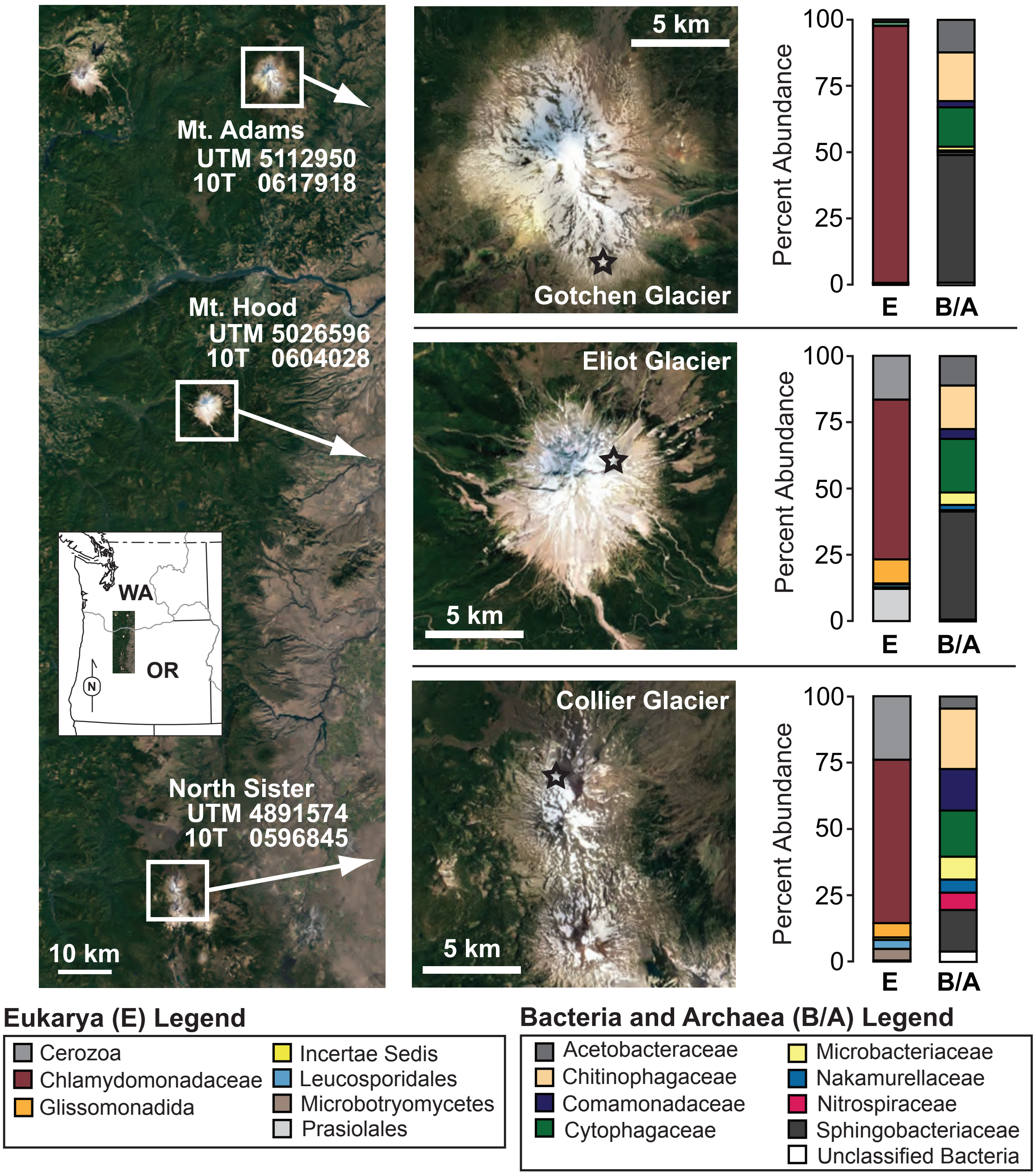

Figure 2. Box-Whisker plots of carbon assimilation rates by supraglacial communities. The horizontal line in each box indicates the median and closed circles represent the mean (n=3 for each treatment). Dark treatments were amended with 100 μM $NaH^{13}CO_3$.