TIOGA PASS REVISITED: INTERRELATIONSHIPS BETWEEN SNOW ALGAE AND BACTERIA

by

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ABSTRACT

Previously (1969-70) snow algae were studied at Tioga Pass, Sierra Nevada, California. Red snow algae were identified; their distribution was patchy; and they were actively photosynthetic. In July-August 1993, red snow patches were abundant in this same area and biological comparisons were made between red and non-colored snow. Algal cells were often about 750 times more abundant in red snow than in white snow; and no chlorophyll was detected in white snow while red patches contained up to 0.1 μgm chlorophyll mL snow^{-1}. Bacterial abundances in white patches were only one-third to one-eighth those in red snow and dissolved organic carbon was also lower. In red snow the incorporation rates of ^{3}H-leucine into bacterial protein were 103-295 times less than algal photosynthesis rates when both were expressed as μgm C taken up mL snow^{-1} h^{-1}. Bacterial production rates were also lower in white snow than in red snow. These results suggest that bacteria were intimately associated with algae in the snow and that bacteria may have been utilizing carbon excreted by the algae. This hypothesis needs to be confirmed by labeling algae with radioactive carbon, isolating the ^{14}C excreted by the algae, and feeding it back to bacteria in snow patches.

INTRODUCTION

Patches of colored snow are very common in temperate and tropical mountainous areas and in the polar regions. According to Kol (1968), colored snow was first noticed by Aristotle. In shaded areas (light cover percentages < 50%), the color is often green (Fukishima, 1963), but the more commonly reported color is red, which occurs in more open, alpine areas.

The color is caused by algae growing in the snow and Kol (1968), in her comprehensive text on microbial snow taxonomy and distributions, lists 354 algal species that occur in snow. However, the most common dominant species is *Chlamydomonas nivalis* Wille. This alga is usually found as blooms of spherical, red spore stages (zygotes), but the cells are initially green and flagellated. The life cycle of this alga is shown in Figure 1 and this cycle apparently follows the water cycle (Hardy and Curl, 1972). That is: 1) blooms of zygote spores occur in old waterlogged snowfields that persist into the summer and they color the snow red; 2) when the snow melts, the spores aggregate into reddish crusts on the soil or on talus rocks; 3) these are covered by fresh dry snow in the winter; and 4) in the spring, when light can penetrate well into the snow (Curl et al, 1972) and the snow water content increases, the red spores form green flagellated cells and gametes that eventually swim up to the snow surface and give rise to red zygote

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spores again. This latter step occurs with sexual reproduction and is possibly an effect of high sunlight intensities and nitrogen deficiency at the snow surface that enhance the formation of carotenoid pigments in the cells. The development of the bloom and quantitative factors that affect it in the field need further investigation and laboratory work on formation of green flagellated stages from the algal crusts is also needed.

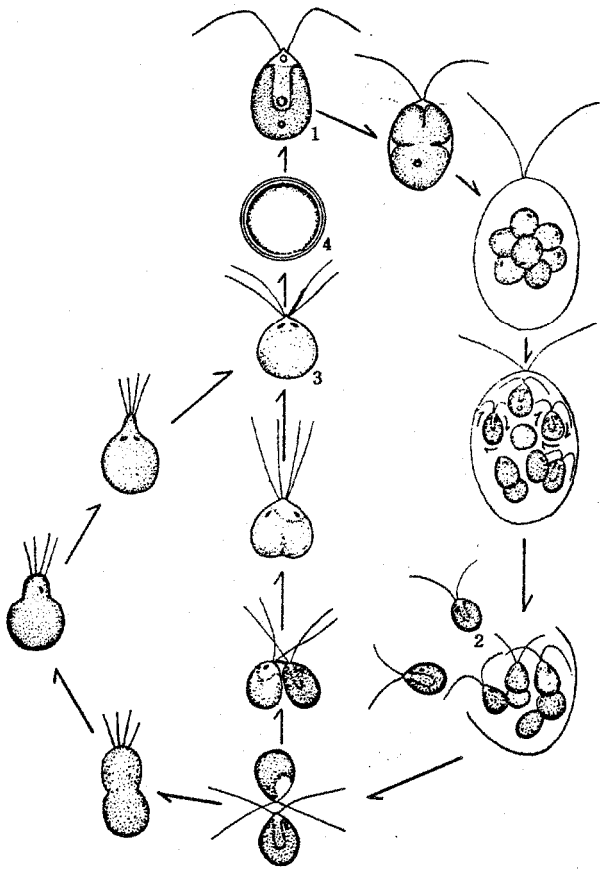

Figure 1. Life cycle of the common snow alga, *Chlamydomonas nivalis*. 1. Vegetative motile cell. 2. Gametes. 3. Motile zygote. 4. Red spore zygote.(after Fukishima, 1963).

Red snow has long been known to occur in abundance in the Tioga Pass area of the High Sierra Nevada, California. It was first noted there by Sharsmith (1935, 1941) and it was reported to me by Heisey (personal communication) that colored snow occurred in the Hall Natural Area for every year for 25 years prior to 1969.

In 1969-70 I carried out an extensive investigation of snow algae in this area and particularly in the Hall. I showed that the distribution of colored snow was extensive throughout the Sierra, that algae near Tioga Pass mostly occurred near the snow surface--but could extend down to 10 cm below the surface, that the distribution of algae was very patchy within a given snowfield, that the main causative species was the alga, *Chlamydomonas nivalis* , and that the algae were actively photosynthetic in that they took up radioactive carbon dioxide when colored snow was incubated *in situ* with this isotope (Thomas, 1972).

Weiss (1983) was the first to study the association between the algae and bacteria in the snow at Tioga Pass. He published scanning electron micrographs showing that bacteria were attached to algal cells, and noted that snow patches that did not contain algae also had no bacteria, although he did not give any data supporting this latter point.

The purpose of the research presented herein was to investigate further the interrelationships between the algae and the bacteria using modern isotope and microscopic techniques. I hypothesized that bacteria were more abundant in snow that contained algae, and that the bacteria were utilizing organic matter excreted by the algae for their growth. If bacterial production was less than that of the algae in colored snow, then this latter hypothesis would be supported; if the bacterial production was greater than that of the algae, then the bacteria would be mainly dependent on wind-blown organic matter, deposited on the snow surface, for their nutritional needs.

Snow algae are known to excrete about 10% of the carbon taken up during photosynthesis (Fogg, 1967). Thus one can envisage a "phycosphere" surrounding each cell where excreted organic matter is concentrated and where bacteria might be abundant. This concept (Jones, 1982) is illustrated in Figure 2.

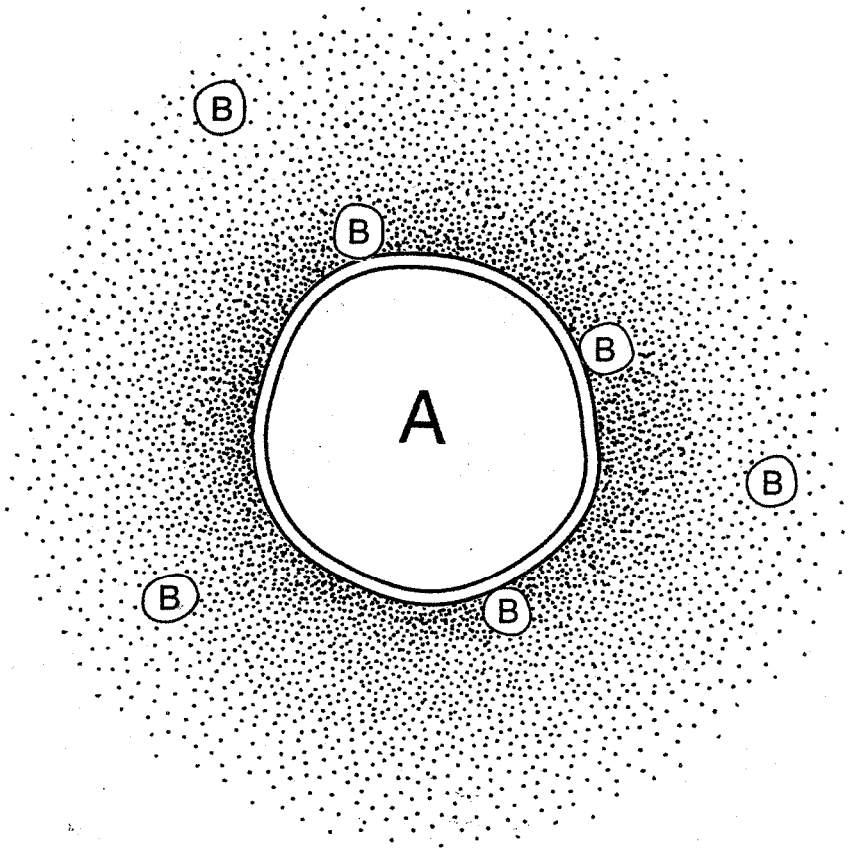

Figure 2. Concept of the "Phycosphere". A. Red algal spore. B. Bacterial cells, attached to spore and free-living. The gradient of small dots represents organic moleculesexcreted by the algal spore.

Since I had previously been able to carry out research on snow algae near Tioga Pass, this area was chosen for the 1993 work, particularly since the snowfields had lingered from a heavy snow season and they were readily accessible from the roads. Also there was a research station about 45 km south--the Sierra Nevada Aquatic Research Laboratory (SNARL)--where laboratory equipment could be set up and samples processed.

METHODS

Locating Colored Snow

We visited the Tioga Pass area in early July for a short scouting trip and found that red snow was very widespread. In early August we identified five sites that had color in the snow. Most of these were easily accessible by short hiking from the car, and I selected the closest sites. One of these, Site "E", was across the dam at Saddlebag Lake at an elevation of 3300 m. Later on we sampled two sites, "F" and "G", that were located on talus slopes above the Lake in the valley of upper LeeVining Creek. These were accessible by water taxi and short hiking.

Sampling and Narrative

During each sampling period (successive weeks), we sampled red and non-colored snow on one day for standing crops of algae and bacteria. The next day we returned to the same snowpatches to assess algal and bacterial production. All samples were taken with sterile 20-mL liquid scintillation vials as was done previously by Mosser et al (1977) except that the samples for snow nutrients were taken in sterile plastic Whirlpac bags. After each field excursion, samples were taken to SNARL for processing. Sampling and incubations were carried out on the following dates: Site E--August 5-6 and August 9-10, 1993; Site F--August 25-26, 1993; and Site G--August 30-31, 1993. At all sites we compared red and non-colored snowpatches.

Standing Crop Measurements

At each site we measured a given volume of snow with a graduated cylinder and melted the snow to determine its water content (density). All parameters were converted to their values per mL of snow.

Bacterial samples were fixed in 5% (final concentration) buffered formalin. At SNARL 0.5 mL aliquots were stained with 1 $\mu g\ mL^{-1}$ (final concentration) of a fluorescent dye, 4'-6-diamidino-2-phenylidole (DAPI), for 10 min. and filtered through 0.2 μm membrane filters. The filters were cleared with oil and mounted on slides which were sealed with clear nail polish. These slides were examined by epifluoresent microscopy (Hobbie et al, 1977) in our La Jolla laboratory and the numbers of bacteria assessed.

Algal samples were fixed in Lugol's iodine solution and their numbers counted microscopically at SNARL using a Palmer-Maloney counting chamber. This process also allowed identification of algal species using the taxonomic figures of Kol (1968).

One-mL samples were filtered through glass-fiber filters for chlorophyll determinations. The filters were extracted overnight in 10 mL of cold 90% acetone and chlorophyll determined fluorometrically with a calibrated instrument. This did not give realistically valid results, because it was later found necessary to grind the filters with a tissue grinder to extract all of the pigments and after this was determined, most samples had been stored in the refrigerator for too long a period. This was not the case with samples from Site G which were processed within one day and I consider only those samples to have given valid estimates of chlorophyll.

Algal and Bacterial Production Estimates

Algal production was measured by adding 0.5 μCi of radioactive ^{14}C-labeled bicarbonate to snow slush samples (approximately 5 mL) in liquid scintillation vials and incubating the vials in the snow for 1 hr in full sunlight (2100 μm quanta m^{-2} sec^{-1} photosynthetically active radiation). Two vials from each snowpatch--red and non-colored--were incubated in the light; two vials were covered with aluminum foil during incubation and these served as dark controls. At the end of the incubation period all vials were fixed with 5% (final concentration) formalin. At SNARL the vials were placed in the fume hood and 50 μL of 1N hydrochloric acid was added to each vial. The vials stood open for 48 hr so that residual inorganic tracer could be removed. Then liquid scintillation fluid was added to them and their organic radioactivity was assessed in our La Jolla laboratory. This process measured total photosynthesis--that excreted plus that in particulate cells. The amount of total carbon fixed was determined from the radioactivity taken up divided by the radioactivity added times the amount of inorganic carbon added from the tracer. This latter value was determined from the specific activity of the tracer rather than being directly measured. Samples taken for nutrient analyses showed that dissolved inorganic carbon in snow was undetectable. This method is essentially that of Thomas (1972) and Mosser et al (1977).

Bacterial production was assessed by incubating vials of snow slush to which 7 μCi of a radioactive amino acid (^{3}H-leucine) was added. Time zero controls were fixed by adding 1 mL trichloroacetic acid (5% final concentration TCA) and after 1 hr incubation the process of incorporation of leucine into cellular protein was stopped by TCA addition. All vials were incubated in the snow and were darkened with aluminum foil. At SNARL the contents of each vial were filtered through 0.45 μm membrane filters which were washed with TCA to remove residual leucine. The filters were dissolved in 1 mL ethyl acetate and liquid scintillation fluid was added to each preparation. Radioactivity incorporated into precipitated protein was assessed in our La Jolla laboratories. The amount of bacterial carbon produced was calculated from the radioactivity incorporated divided by the specific activity of the leucine times a factor assessing the carbon in bacterial protein. This method is that of Simon and Azam (1989).

These procedures allowed comparisons between algal production and bacterial production in red and non-colored snow and between algal production and bacterial production on the basis of carbon produced. Ideally algal production should be measured by the uptake of radioactive gaseous carbon dioxide, but Mosser et al (1977) showed that shaking liquid samples periodically during incubation gives the same results as incubation with the gas. For comparison of leucine uptake from a solution with photosynthetic uptake, it was necessary to have both substrates in the liquid phase. Both algal and bacterial samples were shaken at 10 min. intervals during incubations.

Plant Nutrients in Snow

Samples were taken from Site E for analyses of nutrients in snow meltwater. At SNARL the meltwater was filtered through Whatman #1 filter paper followed by filtration through a 1 μm polycarbonate membrane filter. These filtrates were kept cool and transported to Babcock Laboratories in Riverside, CA for commercial analyses of their nutrient content. Major nutrients and trace metals were analyzed. Also dissolved organic carbon was measured to compare such values in red and non-colored snow.

Algal Crust Sampling

On the last day of sampling we noticed dried reddish-gray algal crusts on the talus rocks below Site G. These were collected in scintillation vials for microscopic examination and are stored in the cold at La Jolla.

RESULTS

Standing Crops

Data from algal and bacterial cell enumerations are shown in Table 1 and comparative ratios are given in Table 2. Algal cells were often about 700 times more abundant in red snow than in white snow and ranged up to 63,000 cells mL^{-1} of snow in colored samples. The algae consisted entirely of red spores--*Chlamydomonas nivalis* and *Trochiscia americana*. The latter species is distinguished by reticulations on the cell walls plus some spines around the periphery of the cells. Although fungi are known to occur in snow, they were rarely seen during microscopic examination of preserved algal samples. In the samples from Site G, no chlorophyll was detected in white snow; red snow contained about 0.1 $\mu g\ mL^{-1}$ of snow. This is about 100 $\mu g\ L^{-1}$ which is well above values found in most aquatic ecosystems.

TABLE 1. Cell Numbers of Algae and Bacteria in Red and White Snow.

DATE	SITE	RED SNOW ALGAE (10^2 cells mL snow^{-1})	RED SNOW BACTERIA (10^3 cells mL snow^{-1})	WHITE SNOW ALGAE (10^2 cells mL snow^{-1})	WHITE SNOW BACTERIA (10^3 cells mL snow^{-1})
8/5/93	E	635	273	0.84	49
8/9/93	E	499	324	0.90	114
8/25/93	F	4.4	178	0.21	63
8/30/93	G	204	169	0.30	20

TABLE 2. Comparative Ratios of Microbial Standing Crops in Snow.

DATE	SITE	RED SNOW Biomass ratio (Algae/bacteria)	WHITE SNOW Biomass ratio (Algae/bacteria)	ALGAE CELL RATIO (Red snow/ White snow)	BACTERIAL CELL RATIO (Red snow/ White snow)
8/5/93	E	4433	32.4	756	5.57
8/9/93	E	2919	15.1	554	2.84
8/25/93	F	46.8	6.33	21.0	2.83
8/30/93	G	2292	28.6	680	8.45

Some bacteria were found in white snow, but the abundances were about one-third to one-eighth of those in red snow. For instance, at Site E on August 5, 1993, red snow contained 273,000 bacterial cells mL snow^{-1} while white snow contained 49,000 cells mL snow^{-1}. This is contrary to the results of Weiss (1983) who found bacteria to be absent from white snow. Some of the bacteria were attached to algal cells, as Weiss reported, but some were also free-living. Biomass ratios based on equivalent cell volumes of algae and bacteria are also given in Table 2. Cell volumes of algae were calculated as spheres having a diameter of 20 μm and those of bacteria were calculated as spheres having a diameter of 0.75 μm. Biomass of algae was 50-4400 times that of bacteria in red snow and 6-32 times that of bacteria in white snow. Thus algae were very abundant compared to bacteria in red snow and less so in white snow.

Dissolved organic carbon was higher in red snow meltwater than in that from white snow. At Site E, DOC was 2.8 and 4.0 mg L^{-1} in red snow on two successive dates, while it was 1.2 and 3.0 mg L^{-1} in white snow. These results suggest that more organic matter may have been available for bacterial growth in red snow than in white snow. No differences were found in dissolved organic nitrogen between red and white snow.

Biotic Production

Data for algal and bacterial production in snow are given in Table 3 and comparative production ratios are given in Table 4. In red snow, carbon production by algal photosynthesis ranged from 1.2 x 10^{-2} µg C mL $snow^{-1}$ hr^{-1} to 12.3 x 10^{-2} µg C mL $snow^{-1}$ hr^{-1}. To compare with literature values (Mosser et al, 1977), these photosynthesis values were divided by algal cell volumes at all sites and by chlorophyll for Site G. Photosynthesis per mm fresh algal volume and per chlorophyll fell within the ranges reported by these investigators for *Chlamydomonas nivalis* snow algal blooms. In white snow, photosynthesis values ranged from 0.00 to 0.16 x 10^{-2} µg C mL $snow^{-1}$ hr^{-1}. Thus, while there was sometimes real photosynthesis in non-colored snow, it was always very much less than that in red snow. Ratios of photosynthesis in red snow to that in white snow ranged from 27 to 79.

TABLE 3. Organic Production Rates of Algae and Bacteria in Red and White Snow.

DATE	SITE	RED SNOW Algal Production (10^{-2} µg C mL $snow^{-1}$ h^{-1})	RED SNOW Bacterial Production (10^{-4} µg C mL $snow^{-1}$ h^{-1})	WHITE SNOW Algal Produciton (10^{-2} µg C mL $snow^{-1}$ h^{-1})	WHITE SNOW Bacterial Production (10^{-4} µg C mL $snow^{-1}$ h^{-1})
8/6/93	E	3.60	2.00	0.000	0.035
8/10/93	E	12.30	8.72	0.150	0.447
8/26/93	F	1.16	1.13	0.017	0.910
8/31/93	G	2.19	0.74	0.080	0.345

TABLE 4. Comparative Microbial Production Ratios in Snow.

DATE	SITE	RED SNOW Production Ratio (Algae/Bacteria)	WHITE SNOW Production Ratio (Algae/Bacteria)	ALGAL PRODUCTION RATIO (Red Snow/ White Snow)	BACTERIAL PRODUCTION RATIO (Red Snow/ White Snow)
8/6/93	E	180	-----	-----	56.4
8/10/93	E	141	33.6	79.0	18.3
8/26/93	F	103	1.87	68.0	1.2
8/31/93	G	295	23.2	27.0	2.2

At all Sites, measurable leucine incorporation occurred and the ratios of algal to bacterial production were higher in red snow as compared with those for white snow. Bacterial production itself was generally higher in red snow than in white snow. An example of these comparisons of algal

production and bacterial production for Site E is as follows: In red snow algal production was 4 to 12 x 10^{-2} µg C mL snow^{-1} h^{-1} while bacterial production was 2 to 9 x 10^{-4} µg C mL snow^{-1} h^{-1}--a difference of about two orders of magnitude. In white snow at the same Site, algal production ranged from 0.00 to 0.15 x 10^{-2} µg C mL snow^{-1} h^{-1} while bacterial production ranged from 0.035 to 0.447 x 10^{-4} µg C mL snow^{-1} h^{-1}--again a very large difference. In red snow at Site E, algal production was 141 to 180 times higher than bacterial production. This suggests that the bacteria were utilizing organic matter produced photosynthetically by the algae.

Snow Nutrients

Except for iron and sometimes zinc, all nutrients were below detection limits. In these commercial analyses, the limits were <0.1 and <0.05 mg L^{-1} for nitrate and inorganic phosphate, respectively and detection limits were <0.01 mg L^{-1} for trace metals. No differences in nutrient content were noted between red and non-colored snow.

Algal Crusts

The discovery of dried algal crusts, occurring on talus rocks below Site G, and left over from snow that had melted, is intriguing. These crusts stained our fingers red when we sampled them and microscopic observation showed that they contained many red algal spores. We attempted to germinate them and obtain green flagellated cell stages by mixing some of the crusts with water and keeping them cold, but so far this stage of reproduction has not been observed. The algae must overwinter as crusts when they are covered with fresh snow, and it has been hypothesized that the flagellated stages come from these crusts and swim up to the snow surface when the snow becomes waterlogged and air temperatures increase in the spring (Hardy and Curl, 1972).

DISCUSSION AND CONCLUSIONS

The evidence presented above suggests that, in the snow, bacteria and microscopic algae are intimately interrelated to each other. The algae may excrete organic matter that the bacteria use and the bacteria seem to be attracted to colored snowpatches. This conclusion was reached by comparing bacterial and algal production rates in red snow and by noting that bacterial abundances were less in white snow than in red snow. It would be interesting to label the snow algae, isolate excreted radioactive organic carbon from the algae, and see if bacteria in the snow would incorporate it into their cellular material. Although bacteria may be promoted by the presence of algae (our present hypothesis), bacteria may also be beneficial to the algae. They may cause mineralization of organic matter to supply inorganic nutrients to the algae, and they may produce vitamins that algae often require.

Various experiments could be carried out with algal crusts. To form green flagellated stages, a cold shock might be necessary, and nutrient solutions could be added. There is a cold room at SNARL where snow could be incubated along with crusts and life cycles of the algae could be studied. It might be possible to culture algae from crusts or from live spores collected at Tioga Pass. Isolation of bacteria into pure culture could be done and such cultures could be mixed with cultured or naturally-occurring algae and bacterial responses assessed.

It appears that our present investigation is mainly preliminary, and much could be done to clarify an intriguing interrelationship between these two biotic groups that co-occur in snow, particularly in regard to following the temporal development of algal blooms from the late spring into the period of complete melting in the summer.

A more general and long-range aspect of snow biotic studies is the possible relationship to acid precipitation. It is known that aquatic ecosystems in the Sierra are sensitive to acidification and snow ecosystems may be no exception to this generalization. In the spring in the Sierra, there are pulses of low pH runoff and this is the time when snow algae become abundant in waterlogged snow. There may be a

relationship between such pulses and the migration of algal flagellated stages up to the snow surface. Experiments could be carried out with algal crustal material to see whether incubation in low pH media stimulates the formation of the flagellated stages. Also following the development of snow algae blooms in the spring in relationship to snow pH might be useful. Possible relationships between the snow alga, *Chloromonas*, and acidity in snow have been discussed by Hoham and Mohn (1985). They studied several species of this genus in cultures and established pH optima for growth.

Furthermore, there may be a relationship between snow algae and climate change. This process may include warming trends and also increases in UV radiation. The latter may have a direct influence on snow algae by the induction of red spherical zygotes from green flagellated stages, and also might influence the overall concentration of algae in summer snowfields. It will be interesting to compare present algal abundances at Tioga Pass with those found in 1969-70 (Thomas, 1972 and unpublished data).

A more practical aspect of snow microbial ecology is the relationship of snow algae to snow albedo. A few measurements indicate that albedo is decreased by about 15% in red algal patches as compared with patches containing no algae (Duval, 1993 unpublished data). However, since the algae occur as patches of red snow in given snowfields and the distribution of algae is highly patchy (Thomas, 1972), the overall albedo values may not change much over a whole snowfield, or at least the values may have a high variance. Such variation remains to be investigated, but if mean albedo values are decreased, then melting of snowfields would be increased, and this effect may be of interest to snow hydrographers.

As can be seen, the results presented herein open up many ideas and testable hypotheses for further investigation of this unique snow ecosystem.

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