

by

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INTRODUCTION

Snow algae are known from alpine environments and high latitudes worldwide (Kol 1968). This report will emphasize semi-permanent snow in forested regions of western and eastern North America. Most snow algae belong to the Division Chlorophyta (green algae) and are responsible for a variety of colorations during snowmelts in spring and summer. Red snow is caused by the green alga, *Chlamydomonas nivalis*, and is prominent in open exposures in our western mountains. Orange snow, usually associated with coniferous tree canopies, is caused by at least three species of the green alga, *Chloromonas*. One of these species, *C. brevispina*, is prominent in the Pacific Northwest (Hoham et al. 1979). A second species, *Chloromonas nivalis*, is widely distributed in all of western USA and Canada (Hoham & Mullet 1977, 1978, Kol 1964). A third species of *Chloromonas*, which is still under investigation, is particularly dominant in southern Arizona, but may be found throughout the west. Green snow, usually associated with heavy shading from coniferous trees or in deeper layers of more open-exposed snow, is also caused by a variety of species of the green algal flagellate, *Chloromonas* (Hoham 1975, Hoham & Mullet 1977, 1978, Hoham et al. 1979, 1983). Many of these species are the same ones that cause orange snow, but in different phases of the life cycle. In some western snow samples, green snow populations may reach levels of 5×10^5 to 1×10^6 cells ml⁻¹ of liquid meltwater. Green coloration of snow is known from the mountains of western North America as well as from New York's Adirondack Mountains and Québec's Laurentian Mountains. Maximum cell counts of populations of green snow in eastern North America are only 25-50% of those reported from western North America (Hoham 1987).

Snow coloration is caused by a variety of algal cell types (Hoham & Blinn 1979, Kol 1968). Generally, green snow is caused by actively dividing cells, whereas orange and red snows are caused by resting spores producing secondary pigment molecules which mask the chlorophyll. Snow algae normally appear in spring or summer. The first appearance of colored snow occurs usually from one to two weeks after the thaw begins. At this time light penetrates through snowbanks probably initiating the germination of snow algal resting spores at the soil-snow interface (Curl et al. 1972). The germination process releases cells which are equipped with locomotory flagella, and this allows the cells to swim in the liquid meltwater located between the snow crystals (Hoham 1975, 1980, 1989). The cells move upward toward sunlight against the water flow. Stages in the life history of a snow alga can be followed using a core sampler and observing those samples using a field microscope. Life histories and developmental stages of snow algae are complex (Hoham 1980), but it is to the advantage of individual species to deplete nutrients in snow. The nutrient depletion probably triggers the sexual process of the life history thus promoting the formation of resistant resting spores. The resting spores become the survival stage on soil or over the forest floor once the snow disappears. These spores remain dormant for about 50 weeks until the cycle is repeated the following year.

Biological Competition between Two Species of Snow Algae

In western Washington's Wenatchee Mountains, green snowbands are prominent in shaded snowbanks under dense forest canopies (Hoham 1975, 1976). These snowbands contain a dominant alga, *Chloromonas pichincha*, and a sparsely found alga, *Raphidonema nivale*. These organisms were isolated into axenic laboratory culture (pure cultures without bacteria) in an attempt to study why one species dominated in nature. It was found that both species could assimilate inorganic and organic sources of nitrogen and phosphorus for growth (Hoham 1980). However, there were selected advantages demonstrated for the dominant alga, *Chloromonas pichincha*, which optimized at a cold temperature (1-5°C), its growth was enhanced by leachate extracts from coniferous leaves, bark and pollen, it optimized in an acid pH (6.0) similar to that found in snow, and this alga failed to demonstrate an exogenous vitamin requirement for growth (Hoham 1975, 1976, 1980). The sparsely found *Raphidonema nivale* optimized over a broad temperature range (1-15°C), its growth was

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inhibited by leached extracts from some of the conifers which grew near the snowbanks containing this alga, its optimum pH was basic (above 7.4), and this alga needed exogenous vitamin B₁ for growth (Hoham 1975, 1976, 1980). *Chloromonas pichincae* has been favoured through natural selection over *Raphidonema nivale* in snowbanks studied in western Washington.

Physiological Ecology of Red and Green Snow

Red snow, caused primarily by *Chlamydomonas nivalis*, is most common in open exposures away from trees or above timberline (Hoham & Blinn 1979, Kol 1968). The primary source of nutrients for red snow is the dust and rock particles that cover the surface of snow in these areas. The secondary red pigments in the cells of *C. nivalis* belong to the keto-carotenoids, and this pigment biosynthesis parallels chlorophyll decomposition as well as nitrogen deficiency in the snow (Czygan 1970). Green snow, usually caused by species of *Chloromonas*, is more typical of shaded snowpacks receiving considerable nutritional input from coniferous debris lying over the surface of the snow (Hoham 1976).

The accumulation of trace metals in snow and in snow algae has been reported from Greenland, Washington, USA and Spitzbergen (Erik Fjordingstad 1973, Erik Fjordingstad et al. 1974, Hoham et al. 1977, Einer Fjordingstad et al. 1978). From these studies it is apparent that snow algae causing green and red colorations of snow have the capacity to concentrate trace metals many thousands of times greater inside their cells compared to what is found in the surrounding snow. This is further evidence that snow algae are interacting with snow chemistry and are influencing changes in snow chemistry during the snow melt. These studies also point out that different strains and species of snow algae may have different nutritional requirements. Thus one should not expect a single growth medium to be satisfactory for growing all species of snow algae used in laboratory studies.

Primary productivity studies using ¹⁴C in the field showed similar amounts of carbon fixed in populations of *Chlamydomonas nivalis* (Fogg 1967, Mosser et al. 1977) and mixed populations of snow algae (Komárek et al. 1973). Thomas (1972) reported higher amounts of fixed carbon for *Chlamydomonas nivalis*, but he also reported a high assay of CO₂ concentration in the snow meltwater. Newton (1982) reported a minimum pH of 6.2 in red snow containing *Chlamydomonas nivalis* whereas control snow lacking algae had a minimum pH of 6.8. The cause of these differences was not known, but it might relate to the metabolism of the alga which could affect the snow chemistry surrounding the cells.

Snow Algae and Snow Chemistry in Eastern North America

The green snow in the Adirondacks of Upstate New York and the Laurentians of Québec is caused by an unidentified species of *Chloromonas*. The Adirondack snow populations were first reported in 1972 (Hoham 1987) and the Laurentian populations were discovered for the first time in May 1988 (Hoham, Jones & Germain, unpubl.) The eastern snow algal species is very closely related to the western North American snow alga, *Chloromonas polyptera*, and through further studies it may be found that all of these populations are part of the same species complex.

Two axenic strains of the Adirondack *Chloromonas* were compared to two axenic strains of *Chloromonas polyptera* from Arizona for pH optima (Hoham & Mohn 1985). The Adirondack strains showed optimum growth over a pH range from 4.0-5.0, whereas the Arizona strains showed an optimum growth in a pH range from 4.5-5.0. Growth was measured using cell counts, cell measurements and absorbance at 440 nm. This study suggested that acid precipitation so prevalent in eastern North America may be selecting for more acidic strains of snow algae in the Adirondacks. At this time, pH studies have not been performed on the Québec snow algal populations.

In a preliminary investigation, snow samples collected in May 1987 from 1265 m and 1341 m on Whiteface Mtn, New York, were analyzed to see if snow algae might be affecting snow chemistry. Two samples were collected from each site, one containing the Adirondack *Chloromonas* and an adjacent control sample lacking the algae. The samples were analyzed at Syracuse University in the laboratory of Dr Charlie Driscoll by his technician, Chris Yatsko. In both sites, the pH was more basic in samples containing algae (5.87 vs 5.63 at 1341 m; 5.17 vs 4.98 at 1265 m). Since the collections were made in mid to late afternoon, these differences may relate to CO₂ consumption during photosynthesis in samples containing algae. Also at both elevations, conductivity was lower in samples containing algae.

implying that nutrients were being metabolized (13.1 vs 19.5 μmhos at 1341 m; 9.6 vs 16.4 μmhos at 1265 m). Nutrients analyzed included SiO_2 , Cl^- , SO_4^{--} , NO_3^- , NH_4^+ , Na^+ , K^+ , Ca^{++} and Mg^{++} . Particularly noteworthy were drops in concentrations of NO_3^- and K^+ in samples containing algae (5.3 vs 9.7 μeq at 1341 m and 8.0 vs 10.8 μeq at 1265 m for NO_3^- 40.6 vs 77.4 μeq at 1341 m and 29.7 vs 63.7 μeq at 1265 m for K^+).

Similar preliminary investigations of the effects of snow algae on snow chemistry were done in the Laurentian Mountains, Québec, in May 1988 (Hoham, Jones & Germain, unpubl.). As reported for the Adirondacks, pH was more basic and conductivity was lower in Laurentian Mountain samples containing algae. Concentrations of SO_4^{--} , NO_3^- and NH_4^+ were lower in samples containing algae compared to control samples lacking algae. Concentrations of K^+ in Laurentian snow did not correlate with data collected from the Adirondacks. These preliminary studies indicate that more careful attention needs to focus on the biological interaction between snow microorganisms and snow chemistry. Too often, snow chemists have examined snow chemistry in the snowpack only at the time of early snowmelt. These reports should stir some interest between snow chemists and snow biologists to investigate the interaction between snow algae and snow chemistry from the time of early snow melt till the complete disappearance of the snowpack. I hope that other investigations will develop in the near future in addition to those reported here.

Other Microorganisms in the Snow Ecosystem

Other organisms should be mentioned to give a more complete picture of the snow ecosystem. Two algae not mentioned previously are the golden alga, *Chromulina chionophilia*, and the colorless euglenoid, *Notosolenus*. The location site of the golden alga is usually in snowbanks associated with coniferous trees (Hoham & Blinn 1979), and the implication is that the coniferous canopy probably supplies critical nutrients for this alga's growth. *Notosolenus* is the only colorless non-photosynthetic alga known from snow (Hoham & Blinn 1979). Its presence is usually sparse in number, but it is found only in snow located directly under tree canopies (Hoham & Blinn 1979). All euglenoids studied under laboratory conditions require vitamin B₁₂, and in addition, many require vitamin B₁ (Leedale 1967). This implies that snowbanks directly underneath coniferous tree canopies must supply enough vitamins for the growth of this colorless alga. Again, whether the vitamins are coming from the canopy itself or from some other source (bacteria in snow, coniferous leachates at the top of the snowbank, lichen pieces or fungi) is not known.

The snow fungi, *Chionaster nivalis* and *Selonotila nivalis*, are found in surface snow. It is not understood how these fungi gets into snow or how they might interact with other organisms. Since they are fungi, they need an external source of carbon. The likely source of carbon is from the photosynthetic algae (*Chloromonas* or *Chromulina*) or from lichen fragments. There is no physical evidence that *Chionaster* or *Selonotila* form any type of lichen association with the snow algae, thus the fungi are probably receiving nutrients passively in snow from algae, bacteria or from coniferous leachates. It is also of interest that there are different distribution patterns of these two snow fungi. *Chionaster* is found on residual snow in the Pacific Northwest, the northern Rocky Mountains, New York State, New Hampshire and Québec, but it appears to be absent from the southwestern United States (Hoham & Blinn 1979). *Selonotila* is prevalent on residual snow throughout western North America (Hoham & Blinn 1979, Kol 1968), but it appears to be absent from eastern North America. It is not clear why there are regional differences in distribution of these two fungi.

Another snow fungus, *Phacidium infestans*, grows throughout melting snowbanks in some parts of the Pacific Northwest (Hoham 1975). *Phacidium*, unlike *Chionaster* and *Selonotila*, is a branching tubular fungus to which many snow algae passively adhere. However, there is no physical connection between the algae and *Phacidium* as would be found in a lichen symbiosis. However, this does not rule out the possibility of an exchange of metabolites between the algae and fungi extracellularly. Upon the complete melting of snowbanks containing snow algae and *Phacidium*, dried strands or threads of the fungus may cover over the bare soil, rocks, low tree branches, shrubs, or lichens and mosses on the soil floor. These dried threads may be covered with thousands of snow algal resting spores. Small pieces of these dried threads may be broken up by wind and dispersed to new localities carrying snow algae with them to new points of distribution. It is also possible that small animals may passively carry this fungus on their feet or fur to new localities for distribution.

Primary consumers, protozoa and rotifers, are part of the snow ecosystem (Hardy & Curl 1972, Hoham et al. 1983, Pollock 1970). These microscopic animals prefer to select and digest green cells over the more brightly-colored orange and red cells (Pollock 1970). Otherwise, little is known concerning the role that primary consumers play in the snow ecosystem. Some questions for consideration include how generally distributed are primary consumers in snow, how much do they deplete snow algal populations, what is their life history and how does it relate to other snow microorganisms, and how do they fit into the overall picture of snow chemistry. In addition to rotifers and protozoa, there are other animals which may be found in association with melting snowbanks. These include nematodes, water bears, snow worms, insects, spiders and mites, birds and larger mammals. The nematodes and water bears may be consumers of detritus, but it is not clear what part, if any, the other larger animal forms may play in the snow ecosystem.

A culture collection of approximately 100 strains of snow algae is being developed and maintained by myself and student assistants at Colgate University. This collection contains several snow algae not mentioned in this presentation. The purpose of this collection is to have available a variety of snow algal species for future laboratory studies. To my knowledge, there is no other collection of cold-tolerant algae of this magnitude being maintained.

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