SNOW ALGAE FROM HIGH-ELEVATION, TEMPERATE LATITUDES AND SEMI-PERMANENT SNOW: THEIR INTERACTION WITH THE ENVIRONMENT

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ABSTRACT

Snow algae have been reported from mountainous regions and high latitudes. Dominant snow algae are green algae (Chlorophyta) belonging to the flagellate genera, *Chloromonas* and *Chlamydomonas*. Light is probably the most important factor regulating the distribution of individual species. In response to light, snow algal cells may produce yellow, orange or red carotenoid pigments. Thus snowfields containing these algae may appear red (open exposure), yellow to orange (partial shading) or green (maximum shading). Using growth media, species have been studied axenically in the laboratory. Results of these studies indicate that nutrients, pH, temperature, light and alleopathic effects from conifers may influence the growth of these organisms. Other studies show that snow algae accumulate trace metals many thousands of times greater inside their cells compared to concentrations found in surrounding snow. In the Adirondack Mountains, New York, acid precipitation may be selecting for acidic strains of snow algae, and populations of *Chloromonas* appear to affect snow chemistry through metabolic processes. Organisms in the snow ecosystem which may affect the growth of snow algae include bacteria, fungi, lichen pieces, protozoa and rotifers. A culture collection of about 100 strains of snow algae is being developed and maintained at Colgate University.

Introduction: Snow algae are known from alpine environments and high latitudes worldwide (Kol 1968). This report, however, will emphasize that work which pertains to semi-permanent snow in forested regions of western North America and the Adirondacks of New York. Most snow algae belong to the Division Chlorophyta (green algae) and are responsible for a variety of colourations 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). A third species, which is still under investigation,

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is particularly dominant in southern Arizona, but may be found throughout the west. Green snow, usually associated with heavy shading from coniferous trees, 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). 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 colouration of snow is known from the mountains of western North America as well as from the Adirondacks of New York.

A variety of algal cell types is responsible for snow colouration (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 coloured 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). 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 pichinchae, 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 pichinchae, 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 requiremnet for growth (Hoham 1975, 1976, 1980). The sparsely found Raphidonema nivale optimized over a broad temperature range (1-15°C), its growth was 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 B_1 for growth (Hoham 1975, 1976, 1980). Chloromonas pichinchae 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 deficieny in the snow (Czygan 1970). Green snow, usually caused by species of Chloromonas, is more typical of shaded snowpacks receiving considerable nutritional imput 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 Fjerdingstad 1973, Erik Fjerdingstad et al. 1974, Hoham et al. 1977, Einer Fjerdingstad et al. 1978). From these studies it is apparent that snow algae causing green and red colourations 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 ^{14}C 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 CO_2 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 in the Adirondacks of Upstate New York: Our first encounter with snow algae in the Adirondacks was in Spring 1972. Green colourations were seen on Mt Marcy, Mt Colden and Whiteface Mtn. The green snow was associated with residual snowbanks usually less than 40 cm in depth. The most prominent algal populations were found in snowbanks on north facing slopes, the snowbanks were protected and often shaded by balsam fir, and the surfaces of the snow were covered with coniferous litter from these trees. In the fifteen years studying populations of green snow on Whiteface Mtn, the most intense population found was 2.7 X 10^5 cells ml^{-1} during May 1979. This, however, is only 25-50% of the maximum cell counts reported for green snow populations in western North America. The green snow in the Adirondacks is caused by an unidentified species of Chloromonas. This species is very similar to two species of Chloromonas from western North America. Chloromonas polyptera is similar, but there are differences in vegetative cell size and resting spore morphology. The Adirondack Chloromonas also shows some affinity to the western Chloromonas nivalis through morphology of the resting spore.

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. However, it could not be ruled out that the differences reported were simply species differences between these closely related species.

In a preliminary investigation, snow samples collected in May 1987 from 1265 m and 1341 m on Whiteface Mtn 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

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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 CO_2 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^+). Again, this preliminary study indicates 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. This report should stir some interest between snow chemist and snow biologist 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 pursuit of such an investigation will develop in the near future.

In addition to *Chloromonas*, there are other microorganisms that live in snow in the Adirondacks. A golden alga, *Chromulina* (probably *Chromulina chionophilia*), was found in several collections in the 1970's. This alga was not found, however, in collections made in 1981 and 1987. At this time it is not clear why *Chromulina* has not been found in recent collections. The question has been raised whether its recent disappearance might be related to acid precipitation or to some other selective factor in the environment. The one strain of *Chromulina chionophilia* in the Colgate University culture collection, strain C-65c, does not grow in media lacking vitamins. It is probable that this golden alga receives exogenous vitamins in snow from leachates from coniferous trees or from bacteria which are present in snow. The location site of this 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.

Another microorganism found in Adirondack snow is the colourless euglenoid, *Notosolenus*. This is the only colourless 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 B_{12}, and in addition, many require vitamin B_1 (Leedale 1967). This implies that snowbanks directly underneath coniferous tree canopies must supply enough vitamins for the growth of this colourless 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.

A fourth microorganism in Adirondack snow is the colourless fungus, *Chionaster nivalis*. This little known organism is found in surface snow, and its developmental stages have been described by Kol (1968). It is not understood how this fungus gets into snow or how it might interact with other organisms. Since it is a fungus, it needs 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* is forming any type of lichen association with the snow algae, thus the fungus is probably receiving nutrients passively in snow from algae, bacteria or from coniferous leachates.

Several examples of microorganisms in Adirondack snow have been presented, and several questions have been raised about their metabolic requirements. Again, it is apparent that if those of us interested in studying snow science want to get a more complete picture, then snow microorganisms must be included. This has particular significance when looking at the interactions between snow biology and snow chemistry.

Other Microorganisms in the Ecosystem: The microorganisms mentioned above for the Adirondacks are also found in snow in western North America and elsewhere (Hoham & Blinn 1979, Kol 1968, Stein 1963). In addition, other organisms should be mentioned to give a more complete picture of the snow ecosystem. Another snow fungus, *Selonotila nivalis*, is also found in surface snow. In one example, it was found amongst volcanic ash particles in Glacier National Park, Montana, from the 18 May 1980 eruption of Mt St Helens, Washington. However, it is much smaller than *Chionaster nivalis*, but still possesses the radiating arms so characteristic of both of these fungi. Individual arms in *Selonotila* may be only a few 5m in diameter. As is the case for *Chionaster*, it is not clear what role either of these fungi play in the exchange of nutrients. In April 1987, it was observed that clusters of *Selonotila* were found at the periphery of unidentifiable brown spheres in Arizona snow. Attempts to identify these spheres were futile, but there is the posssibilty that they may have been pollen grains from vascular plants and some type of parasitism was occurring. However, this needs further verification. Snow algae (*Chloromonas*) found in the same Arizona snow samples did not have this type of an association with the snow fungus, *Selonotila*. 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 and New Hampshire, 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 the northeastern United States. 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-coloured 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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