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Ecology of snow algae

1. Introduction

Snow algae represent a very interesting group of organisms, as they live actively at about 0°C, while other plants markedly reduce their living processes or even die at this temperature. They are also able to tolerate frost, and a long-lasting shortage of light, or its excess, during the period of polar night or day, respectively. Despite the numerous investigations carried out, many problems concerning the taxonomy of snow algae and also their biology, ecology and mechanisms of adaptation to life under specific conditions have not yet been explained.

The aim of the present paper is to review the current state of knowledge of the ecology of snow algae.

2. General characteristics of snow algae

About 460 species and varieties of snow algae have been identified, green and blue-green algae prevailing. Diatoms, euglenae, chrysophytes and dinoflagellates are also found in smaller numbers (Kol 1968).

In the ecological aspect, the following groups of algae can be distinguished: Cryobionts, a group of special inhabitants of the cryobiootope, which find the optimal living conditions in this environment, and which are the main subject of the present paper. There are also cryophiles, organisms frequently occurring in the cryobiotope environment, and cryoxenes, which have found their way into the cryobiotope accidentally.

The profusely developing algae colour the ice and snow-fields to various shades of red, yellow, yellowish-green, green, blue and purplish-brown. "Red snow" is the most common, and is caused, among other things, by the development of *Chlamydomonas nivalis*, *Ch. sanguinea*, *Smithsonimonas abbotii*. "Green snow", caused by the development of species of the genera *Koliella*, *Raphidonema*, *Carteria*, is also common. "Yellowish-green snow", caused by the development of *Chloromonas rostafiński* is rare, as are also "yellow snow", due to the blooming of *Cystococcus nivicolus*, and "blue snow", caused by the mass development of *Dactylococcopsis hungarica*.

Purplish-brown colouring is attributed to blooms of *Ancylonema nordenskiöldii*, a species typical of permanent ice.

The composition of "black snow" is not precisely known, it can be both of biogenic and abiogenic origin.

3. Environmental factors with respect to the development of snow algae, adaptations, interrelationships.

Snow algae live in an environment described as a cryobiotope. This can mean both permanent and periodic snow and ice on land and sea. It is best developed in polar regions and in high mountains, where there is an enormous amount of accumulated ice and snow.

3.1 Temperature

The temperature of melting snow which gathers on the surface of the cryobiotope, varies within a very narrow range around 0°C, independently of the air temperature (Kol 1968, Komárek et al. 1973). At a depth of 5 cm below the surface of the snow, the temperatre does not rise above 0°C, while above the patches of snow the temperature gradient is sometimes very sharp, the temperature rising by several degrees centigrade over a few centimeters (Komárek et al. 1973).

The temperatures required by particular species of snow algae are not yet exactly known. In his laboratory experiments, Hoham (1975a) differentiated between true snow algae which did not grow at temperatures above 10°C and their optimum growth occurs at lower temperatures. Their occurrence is probably limited to the cryobiotope. The algae whose development is observed up to 15°C could not be classified as true snow algae, because they could not only grow in snow, but also in the soil and in Alpine lakes. Komárek et al. (1973) isolated algae from samples collected in permanent snowfields. These strains of algae differed in the temperatures required. *Scotiella nivalis* and *Chlorella minutissima* were found to live in a wide range of temperatures, varying from 0—20°C, while *Koliella tatrae* and *K. nivalis* were stenothermic, with the optimum temperature below 10°C. Temperatures above 10°C were usually lethal for these species.

The question arises, how it is that snow algae adapt to low temperatures, resist frost, and are able to assimilate and develop at temperatures around 0°C. The problem has not yet been fully explained, only some general suggestions have been made. Plants survive frost owing to the hardening-off which takes place during the over-cooling of organisms. This is based on changes in the properties of the protoplast which undergoes gradual gelation, thus protecting the cells against deformation. At the same time, the permeability of cell membranes to water increases, this facilitating its migration during over-cooling, and preventing the formation of ice-crystals in the cell. Owing to the growing content of sugar in the tissues, the osmotic pressure of cell sap rises, causing the freezing temperature to decrease and increasing the amount of bound water, which cannot freeze (Michniewicz 1977). Thick cell walls also efficiently protect the cells from freezing. After thawing algae brought from the field and stored in a freezer, the vegetetive cells were found to be deformed, with the pigment concentrated in a drop at the margin of the cell. The cells with thick walls (aplanospores) did not undergo any changes, and initiated a new population (Kawecka 1981).

Even less is known about the mechanisms of the active life of algae at temperature around 0°C. Marrè (1962) suggests that there occurs an increase in the efficiency of all the cell's basic enzymatic mechanisms, this preventing a decrease in the rate of chemical reactions. He also thinks it is possible that the activity of snow algae is limited to the period of high light intensity when part of the solar energy can be converted into thermal energy, raising the temperature of the cell above the temperature of the environment. With respect to this problem, some interesting observations carried out in situ on *Chlamydomonas nivalis* should be mentioned (Fjerdingstad et al. 1978). It was found that every specimen seemed to be set in a small depression melted down in the surface of the snow crystal. The authors suggest that the algae melt into the ice surface owing to their high potential of absorbing light energy. Being set in these tiny niches and continuously absorbing light energy, the snow algae produce a microhabitat in which the temperature increases and stabilizes. The surface of the snow crystals is washed by water, this securing the inflow of mineral salts and gases. At the same time the algae are not washed out, being well anchored in the ice.

3.2. Light

The light conditions in the cryobiotope are rather complex. The intensity of light increases with the altitude above sea level and hence in high mountains it reaches particularly high values, and contains a considerable proportion of ultraviolet radiation, which is harmful to life. In the Arctic Zone on the other hand, there occur periods of several months when the sun does not set (polar day) or does not rise (polar night). The amount and quality of light changes as it penetrates through the cryobiotope. Curl et al. (1972) found that the depth to which the light radiation can reach, increases with the density of snow; 1% of the solar energy penetrated to a depth of 18 cm in winter and to 110 cm in late summer, when the density of the snow was close to maximum.

Light rays penetrating the substrate are not uniformly absorbed. Hoham (1975 b) found that blue, red and far red rays are first to be absorbed, already at a depth of 10—25 cm. Green rays and total irradiation reach a depth of 50 cm in the cryobiotope. However, in a later study, Hoham and Mullet (1977) stated that there are sufficient data to suggest the penetration of all wavelenghts of light through snow layers of 70—110 cm.

Snow algae develop in both sunny and shaded sites. They gather on the surface of the cryobiotype and penetrate into the substrate.

Algae forming red blooms can be described as photophilous. They can frequently be found in sunny sites, developing mainly on the surface or immediately under it (Kol 1969, Paryski 1951, Siemińska 1951, Thomas 1972). In the case of very strong insolation they migrate under the surface of the snow, due to which the colour of the snow becomes paler (Kawecka 1978). Stein and Broke (1964) state that during a clear, sunny day the algae are almost invisible.

The algae which produce green blooms occur most frequently in the shade or deeper down in the substrate; they can be described as shade-loving. Hoham (1975 b) observed "green snow" near a forest border on cloudy days. It was found at a depth of 2—24 cm, and does not occur in open space above the tree line. Hoham and Mullet (1977) found *Chloromonas cryophila* on the surface of the snow in open or shaded spaces, and at a depth of 1—42 cm. *Chloromonas rostafiński* developed in shaded and in sunny spaces, but in sunny patches of snow it was found only on cloudy days. When the sun appeared, this alga immediately migrated into deeper layers of the substrate (Kawecka et al. 1979). *Koliella tatrae* and *Chlamydomonas* sp. were found in the cross-sections of the snow in places where the intensity of light was low $(0.2)-0.6-(1.0)\cdot 10^{-2}$ $\mathrm{cal\cdot cm^{-2}\cdot min^{-1}}$. This finding suggests that their occurrence under the snow surface did not result from the mechanical transport of cells with the water produced from the melting snow, but this really was the zone of optimum conditions of light and temperature for these species (Komárek et al. 1973).

It is worth noting that the algae which gather at sunny places have a carotenoid red pigment astaxanthin ($C_{40}H_{52}O_4$) in their cells. Most probably, it plays the role of a protective filter against ultraviolet radiation and the intensity of light significantly affects its production (Fott 1959, Fukushima 1963, Kol 1968, Fjerdingstad et al. 1974). Fukushima (1963) observed that the colour of the snow depends both on the intensity of light and on the time of insolation, With an exposition of 10 min to 7 hours the snow was green, above 7 hours its colour changed to yellowish or brownish, and the red colouring appeared after probably 10 hours or more.

According to Kol (1968, 1975), the pH of the snow is important in the formation of red colouration. He found red cryoseston to develop at a pH of 4.5—5.8, and a green one at a pH of 6—6.5. However, a number of observations do not support this theory (Fogg 1967, Fukushima 1963, Garric 1965, Hoham 1975 b, Hoham and Mullet 1977, Kawecka 1978, Kawecka et al. 1979).

We still do not know how algae can exist under conditions of a high light deficiency, under a thick layer of ice, and also during the polar night. A number of views have been expressed on the subject. Bunt (1963) and Bunt and Wood (1963) emphasise the extreme capacity which algae have to live in conditions of shading. It is also suggested that the organisms change to the heterotrophic mode of nutrition (Rodhe 1955, Wilce 1967), however the studies of Horner and Alexander (1972) and also of Bunt and Lee (1972) indicate that the heterotrophic metabolism does not play a significant role as a source of energy. Wright and Hobbie (1966) also suggest that Arctic algae may utilize the material stored in their cells.

3.3. Nutrients

Large amounts of inorganic matter in the cryobiotope are brought by wind; they originate from industrial dusts, coniferous trees, an weathering mother rocks. Thus, the amount of nutrients depends on the position of the cryobiotope, and is strongly differentiated.

Komárek et al. (1973) found that snows in the Slovak Bielskie Tatra Mts (1340 m) contained large amounts of N and P, and could be compared with the eutrophic waters in the aspect of fertility. A large content of N-mineral and phosphate was also found in snows from the Polish High Tatra Mts (2080 m) (Kawecka 1978), while in the snow from Mt Rainier National Park (USA, 1387 m) these components occurred in smaller amounts (Hoham and Mullet 1977). Fjerdingstad et al. (1974, 1978) carried out chemical analyses of the snow from Spitsbergen and Greenland, and noted fairly large amounts of Ca, Cl, Si, Fe and K, and also of microelements such as Ba, Ti, Pb, Cu, Zn, Cr, Mo, Mn, etc. in the environment. Drifting ice is rich in mineral and organic components when it originates from a shelf, but poor if formed in open waters (Melnikov 1980).

Numerous authors reported that the pH of water from melting snow varied from 3.8 to 7.0. The content of CO_2 did not exceed 5 mg/l (Hoham 1975 b, Hoham and Mullet 1977), and the content of O_2 was fairly small and reached 9—13 mg/l (Hoham 1975 b).

Fjerdingstad et al. (1974, 1978) examined the content of chemical components in the "red snow" in Greenland and Spitsbergen, and found that chemical elements accumulated in the cells of *Chlamydomonas nivalis*. Such elements as Si, Cl, Fe, Ca and K occurred in high concentrations both in the snow and in the algae (Fjerdingstad et al. 1974). The amount of Fe was almost constant, and independent of its content in the environment. This suggests that Fe plays a vital role in the growth of this alga. Many microelements, such as Cu, Mn, Ni, Pb, Zn, Cr, Mo and also such rare metals as La, Ce and Eu, were found in the cells of the algae.

3.4. Ice as an ecosystem

The drifting Arctic ice described by Melnikov (1980) is an interesting ecosystem. An interdependence between the cryobiotope and cryobionts can be observed there, the drifting ice having an autochtonous flora which develops on the surface of the cryobiotope. The main species here are *Chlamydomonas nivalis* and *Ancylonema* sp. The development of algal blooms affects the condition of the ice, which becomes more wet, less transparent, and in its crystalline structure there appear pores, fissures and holes filled with meltwater. In the summer, this water, together with the organisms, runs from the surface down into the ice, where it re-freezes and becomes part of its structure. As the process of melting proceeds in the drifting ice, the layers with the embedded algae may find their way to the surface and give new generations in the next season.

The drifting ice also has an allochtonous flora from the sea water. It is composed mainly of diatoms (*Melosira arctica*, species of *Fragilaria*, *Nitzschia* and *Gomphonema*). They aggregate at the water-ice boundary, where there is most light. Colonial associations form here, the density of cells greatly exceeding that in the sea water. Stratified ice encloses diatoms in its crystalline structure and integrates them into the dirfting ice-floes. With the growth of the ice, the diatoms pass into upper layers and die there.

4. Survival, blooms, productivity

Snow algae can survive unfavourable conditions as resting cells, akinetes aplanospores or hypnozygotes, usually covered with snow or living in the soil. The factors which induce the germination of zygotes and resting cells are not clear. It is not known whether they require a particular quantity and quality of light, dissolved gases, nutrients or water. The zygotes of *Chloromonas cryophila* germinated after about 100 days from when they were produced, and after the first strong frost (Hoham and Mullet 1977).

Also for the resting spores of *Chlainomonas rubra* (Hoham 1974) and zygotes of *Chloromonas pichinchae* (Hoham 1975 b), a long period of dormancy and freezing were found to be indispensible for germination. Curl et al. (1972) and Hoham (1975 b) suggest that light could be the decisive factor initiating the development of resting cells. After germination, the cells produced migrate to the surface. It is possible that this migration is brought about by a particular wavelength and intensity of light (Hoham and Mullet 1977).

The blooms of snow algae appear most frequently in July and August, and fairly often in February, March and June. No blooms were reported to occur in October and November. They are produced when the air temperature remains above 0°C (Fukushima 1963, Hoham 1975 b). The water which gathers on the surface of the cryobiotope seems to be indispensible for the development of the algae (Stein and Amundsen 1967, Pollock 1970, Kawecka 1978).

Fogg (1967), Romanenko (1971), Thomas (1972) and Komárek et al. (1973) examined the productivity of snow algae. The lowest productivity was found by Fogg (1967), 0.000002—0.000864 C mg/mm^3/cell/hr; this value is several times lower than that found in the extremely oligotrophic lakes of Swedish Lapland. A higher productivity was recorded by Komárek et al. (1973): (0.04) 0.13—0.88 (1.85) $C_{ass}\mu g/mm^3$ of algae$^{-1}\cdot h^{-1}$, that corresponds to values found for "sun phytoplankton" of mesotrophic water bodies.

5. Vertical and geographical distribution of algal communities

Snow algae are found from an altitude of 0 m on the coasts of the Arctic Zone to about 5000 m in high mountains. Kol (1968) suggests that there occurs a correlation between the altitude above sea level and the nature of coloured snow, and differentiates between the cryovegetation of Central Europe at 0—500 m, between 500 and 1000 m, and above 1000 m. It is also stated that "red snow" has the widest distribution, occurring from 0 to 4500 m, "green snow" is found up to 3500 m, and the very rare "blue snow" is recorded at a height of 900 and 2000 m.

There are distinct differences in the geographical distribution of snow algae over the Northern and Southern hemispheres. The list given by Kol (1968) shows that of 86 cryophiles, 80 were found in the Northern hemisphere, 22 in the Southern one, and 18 species were common to both hemispheres. *Chlandomonas myvalis*, one of the most common snow algae, occurs only in the Northern Hemisphere, while in Antarctica, the red cryoseston consists chiefly of *Chlamydomonas antarcticus*.

The green cryoseston is composed of a large number of species. Every continent and even different mountain regions have a specific type of green cryoseston. In the Alps and Carpathians it is caused by the development of species of the genera *Carteria*, *Koliella* and *Raphidonema*, also *Chlamydomonas*. In North America the green cryoseston consists of *Chlamydomonas yellowstonensis*, in Japan it is *Cryocystis japonica*, and in Antarctica — *Chlorella antarctica* and *Stichococcus bacillaris*. Without doubt the cryoseston of the world is not yet adequately known. However, Kol (1968) suggests that among snow algae, there are species endemic to the Carpathians, the Alps, the Caucasus, North and South America, Antarctica, Greenland and Japan.

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