THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: VII. THE ECOLOGY OF THE ALGAE OF SITE 1, A MOSS TURF

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Abstract. The population dynamics of 11 species of algae occurring in two dominant mosses, *Chorisodontium aciphyllum* and *Polytrichum alpestre*, were followed over a 15 month period at a moss-turf site (SIRS 1). The vertical distribution, both in deep cores and in the upper 1·5 cm. of the turf, was examined by direct observation and culture methods. Horizontal variations in the algal flora, both qualitative and quantitative, were determined. Other aspects of the ecology of the algae were studied in less detail. The results are discussed, relating spatial and temporal changes in the qualitative and quantitative composition of the algal flora to the environmental conditions. The importance of the algae in relation to the general ecology of the ecosystem is discussed.

The Signy Island terrestrial reference sites (SIRS) were established so that gradual accumulation of data on the organisms occurring there would reveal the functional relationships of the various components, leading eventually to total ecosystem analyses. The two sites are contrasting moss communities typical of the maritime Antarctic (Gimingham and Smith, 1970) and widespread on Signy Island. SIRS 1 is an example of a *Polytrichum alpestre–Chorisodontium aciphyllum* turf and SIRS 2 is a *Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* moss carpet; both have been described in some detail by Tilbrook (1973). The present paper is concerned with the ecology of the terrestrial algae of SIRS 1, particularly the seasonal changes in numbers and their vertical and horizontal distribution within the site. The ecology of the algae of SIRS 2 is described by Broady (1977*a*).

Methods

Identification of the algae

Three techniques were used for the examination of the algal flora and the subsequent identification of its components, namely the direct examination of material immediately after sampling, moist-plate enrichment cultures (Lund, 1945), and the culture of algae on mineral nutrient agar plates using Bold's modified Bristol's medium (BBM) (Chantanachat and Bold, 1962). These methods are more fully described by Broady (1977*b*) and the terrestrial algae found in a wide variety of sites are identified and the soil algal communities described.

Vertical distribution of the algae

In deep cores. Single cores were taken from a mixed *Polytrichum–Chorisodontium* turf in August 1972, and from each of a pure *Polytrichum* turf and a *Chorisodontium* turf in March 1973 and January 1974. In summer, they were taken with a simple cylindrical corer, 10 cm.^{2} in cross-sectional area, by pushing it into the soft moss and underlying peat. In winter, a similar corer with a toothed cutting edge was used to cut through the frozen moss and peat. This was rotated by an electric drill with power supplied by a portable generator. The cores were returned to the laboratory intact in sterile aluminium containers. They were then divided into 1·5 cm. long sections, to a maximum depth of 9·0 cm. Each section was examined by a technique similar to that used by Baker (1970) in his study of the yeasts and bacteria from a Signy Island *Chorisodontium* turf. The sample was homogenized for 2 min. in 100 ml. of sterile water at maximum revolutions (14,000 r.p.m.) in a M.S.E. homogenizer. The homogenate was diluted by factors of 10, 10^2, 10^3 and 10^4. For each dilution four aliquots each of five drops were transferred to a BBM 2 per cent agar plate (divided into four quarters) using Pasteur pipettes calibrated to deliver 0·029 ml. $\pm$ 4·5 per cent per drop. The drops were delivered from pipettes held vertically 2 cm. above the agar surface. The agar plates had been previously dried at 70° C for 1 hr. The drops were absorbed into the agar within a few hours. The plates were incubated at laboratory temperature (*c.* 18° C) for 3 weeks, under constant illumination supplied by four 30 W daylight fluorescent tubes. On completion of the incubation period the plates were examined under a binocular microscope at $\times$10 magnification. The

first dilution, giving less than 150 colonies per aliquot, was counted. The colony counts were extrapolated to give an estimate of the numbers of algae per cm.^{2}.

In the upper layers of the moss and peat. Three techniques were used for investigating the distribution of the algae in the upper parts of the moss.

i. *Thin slicing of cores.* One set of summer samples (March 1972), comprising five cores of mixed *Polytrichum–Chorisodontium* turf, was removed using 10 ml. plastic disposable syringes from which the plunger was removed, the nozzle end cut away and the exposed edge sharpened. The cores, 1·4 cm.^{2}, were taken to a depth of about 5 cm. Each core was treated in the following manner. The plunger was introduced into the cut end of the syringe and used to push the core out until the top 2 mm. of the core were exposed at the other end. The surface of the core was pressed gently against the surface of a BBM agar plate for a few seconds. The top 2 mm. section was then sliced off, using a flame-sterilized razor blade, and discarded. The next 2 mm. section was exposed and the process repeated. This was continued as far down the core as possible, on each occasion pressing the newly exposed surface against a sector of a divided agar plate. The plates were incubated and the algal colonies transferred from each exposed surface of the core were counted.

ii. *Culture of algae from individual moss leaves.* In the first experiment ten *Chorisodontium* plants were examined. The lower brown leaves of each plant were removed using flame-sterilized forceps. Commencing with the lowest green leaf (usually 7–10 mm. from the apex of the shoot), every second or third leaf (i.e. a total of seven leaves and the terminal rudimentary leaf) was removed from the stem and placed on a sector of a dried and divided BBM agar plate. Two drops of sterile water were placed on each leaf which was then agitated and macerated as much as possible using fine forceps. Also cultured were 16 4–6 mm. long sections of shoots of the foliose liverwort *Cephaloziella varians* which occurs most abundantly amongst the *Chorisodontium* shoots at a depth of about 8 mm. Each portion was approximately equivalent in length to a *Chorisodontium* leaf.

A similar experiment was performed with *Polytrichum*. All the healthy leaves of six plants were plated (12–24 per plant), the lowest green leaves occurring 3–4 mm. down the stem. The lower brown *Polytrichum* leaves from 4–8 mm. depth were also cultured, but the high numbers of algae in this part necessitated the use of a dilution technique. Each leaf was placed in 10 ml. of sterile water in a MacCartney vial which was then shaken vigorously, by hand, 25 times. 1 ml. of the supernatant was removed and pipetted on to a previously dried BBM agar plate.

In all the above experiments the plates were incubated for 3 weeks at room temperature in constant light as described earlier, and the algal colonies were then counted.

Seasonal changes in algal numbers

Regular counts. Two areas (A and B) of the site were chosen for regular sampling, each consisting of a strip of moss turf 5 m. by 1 m. containing pure and mixed areas of the two mosses, areas of bare eroded peat and a few areas where the moss or peat was encrusted with epiphytic crustose and fruticose lichens. The strips were within the original transects comprising 150 1 m. squares marked out when the site was established (Tilbrook, 1973).

At each sampling time three randomly selected cores of each moss species were removed from both areas. In summer, the cores were easily removed using a cork borer of 1·5 cm.^{2} cross-sectional area. In winter, the power drill and 10 cm.^{2} corer were employed. After thawing the larger cores were sub-sampled in the laboratory using the small cork borer. Only the top 1·5 cm. was homogenized.

The samples were taken at approximately monthly intervals over a 15 month period starting in early summer (November 1972) and continuing until late the next summer (February 1974).

The plate culture count described earlier was used. The cores were treated on the day of sampling. After incubation the colonies on appropriate dilution plates were counted. Random colonies were removed from these plates and identified microscopically in order to calculate the proportions of the different species.

Algal re-colonization of a cleared area of moss. In November 1973, a small area of predominantly *Polytrichum* turf *c.* 1,000 cm.^{2} was cleared of the green vegetation by slicing off the surface 2 cm. of moss shoots. The area was sampled on the day of clearance and at intervals of from 2 to 4 weeks throughout most of the summer. On each occasion ten random cores (1·5 cm.^{2}) were removed, allowing a 2 cm. border of peat around the periphery unsampled in order to minimize edge effects. The algae in the 0–1·5 cm. layer of each core were counted using the plate-culture count method. Randomly selected colonies were removed for identification and assessment of the proportions of the different species.

Observations on slides buried in peat. About 20 clean, sterile glass microscope slides were placed horizontally into the moss until the upper edge was level with the apices of the moss shoots. The slides were introduced at the beginning of the summer (November 1972) and removed twice for the microscopic examination of algal growths. The first removal of half the slides was made only 3 hr. after the slides had been introduced in order to determine how many algae were mechanically deposited on them as a result of pushing the slides into the moss. After 4 months, towards the end of the summer (March 1973), the remainder of the slides were removed. They were transported to the laboratory in staining dishes containing moistened cotton wool to prevent drying out before microscopic examination. One side of each slide was wiped clean; larger adhering portions of vegetation were removed from the other side with fine forceps and a coverslip was put in position. Water was carefully introduced below the coverslip. The slide was microscopically examined at × 100 and × 400 to determine the form and abundance of the algae.

Horizontal distribution of the algae

Culture counts. The moss banks of SIRS 1 were not homogeneous in floristic composition. On each of the sampling times described below 1·5 cm.^{2} cores were removed from contrasting areas and plate counts were performed on the upper 1·5 cm. Randomly selected colonies were removed from the plates and a quantitative assessment made of the algal species present.

The sampling sites were chosen as follows:

i. Five widely separated 1 m.^{2} areas each containing *Polytrichum*, *Chorisodontium* and some bare peat. One core of each category was removed from each square in October 1972.

ii. A 1 m.^{2} area of almost pure *Polytrichum*. Four cores were taken in November 1973 from dense moss cover with *c.* 50 shoots per cm.^{2}, four from a more open moss growth with *c.* 16 plants per cm.^{2} and four from bare peat.

iii. In one part of the site it was noted that small circular areas of bright green healthy *Polytrichum c.* 5–10 cm. in diameter were surrounded by a yellow-brown growth of moribund moss. Five cores were taken from each of these two types of growth, twice during the summer (November 1973 and January 1974). On the latter occasion the moss shoots from both sets of samples were examined microscopically and the areas of photosynthetic green and non-photosynthetic brown tissue were noted.

iv. On the more exposed areas of *Chorisodontium* banks, particularly where the wind funnelled between rock outcrops, there were areas of rippled moss growth, a phenomenon described by Smith (1972). On the windward side of the small ridges, moss growth was prevented by the scouring action of wind-blown ice particles. On the sheltered leeward side, healthy moss growth occurred. Such a rippled area of *Chorisodontium* was sampled in November 1973 when six pairs of cores were removed, one of each pair from opposite sides of the same ridge.

v. Certain areas of the moss banks had a varying cover of epiphytic crustose and fruticose lichens. The dominant fruticose species were *Sphaerophorus globosus*, *Usnea antarctica* and *Alectoria* spp. (Tilbrook, 1973). In November 1973, six pairs of cores were removed from 1 m.^{2} area of *Chorisodontium* partially covered by *Alectoria* spp. One of each pair was taken from a lichen-free area and the other from an adjacent portion of moss overgrown by dense lichens.

vi. Along the lower edge of the moss banks pieces of moss and peat periodically fell away, exposing a vertical or overhanging edge of loose fibrous peat. In November 1973, six cores were taken from the edge of peat and six from the healthy *Chorisodontium* on the surface of the bank immediately above. A second set of six cores was taken in December 1973 from bare peat which had a green algal growth on the surface.

vii. During the major snow melt in early summer rivulets of water flowed over the moss surface where the underlying peat was still frozen. At the height of the melt period (early November 1973) six cores were taken from pure *Chorisodontium* within a melt rivulet and another six from adjacent dry moss. Similar cores were taken from an area of pure *Polytrichum*. The *Chorisodontium* was re-sampled in mid-summer (January 1974) when no melt water had flowed over the surface for about 7 weeks. The cores were taken from positions immediately adjacent to those removed on the previous occasion.

Observations on macroscopic algae. In some areas of the site there were gelatinous growths of algae. Their distribution was noted and they were cultured as described earlier and examined microscopically.

Other aspects of algal ecology

Interactions of algae with other members of the micro-flora. During direct observation of freshly collected material, and of slides buried in the moss and peat, any associations noticed between the algal cells and bacteria or fungi were described and drawn.

Algae as a food source for soil invertebrates. Observations were made on the possible utilization of algae as a food source of Protozoa and Collembola. Notes and drawings were made of the Protozoa during examination of the moist-plate enrichment cultures. More detailed work was performed on the Collembola, in particular the dominant species *Cryptopygus antarcticus*. Gut contents were examined, and guts and faeces were cultured.

Losses of algae in snow melt water. The water in the streams and rivulets produced by melting snow at the end of winter was examined for the presence of algae washed from the moss and peat. Three sets of melt-water samples were collected. At the end of the 1972 winter (November) four samples were taken in sterile MacCartney vials from each of two different streams flowing over the site. Similar samples were collected at the end of the 1973 winter (October) when one sample was taken from each of ten streams and rivulets at the start of the melt period, and again at its termination in November. Later in the season such streams and rivulets were generally absent. Four replicate five-drop aliquots of each sample were pipetted on to BBM agar plates using calibrated Pasteur pipettes. Colony counts were extrapolated to give an estimate of the numbers of algal propagules per ml. of melt water.

Results

Identification of the algae

Eleven species of algae were found at SIRS 1. Following the classification of Bourrelly (1966, 1968, 1970), they were identified as:

Cyanophyceae	*Aphanocapsa* cf. *montana* Cramer; *Nostoc muscorum* Kuetz.
Xanthophyceae	*Ellipsoidion* cf. *perminimum* Pascher; *Monodus subterraneus* Boye Pet.; an unknown species of Pleurochloridaceae.
Euchlorophyceae	*Chloromonas* sp.; two unknown species of Radiococcaceae (designated A and B).
Zygophyceae	*Cylindrocystis crassa* De Bary.
Ulothricophyceae	*Stichococcus bacillaris* Naeg.; *Gongrosira terricola* Bristol.

Illustrations and descriptions of these species are given by Broady (1977*b*). *A.* cf. *montana*, *N. muscorum* and *C. crassa* never appeared in cultures of material from this site, although the first two could grow on the medium employed as shown by their growth from samples from other sites (Broady, 1977*a*). All three were rarely observed during microscopic examination of field material and moist enrichment cultures. The remaining eight species all appeared in BBM agar cultures and were isolated into uni-algal culture for their identification.

Vertical distribution of the algae

In deep cores. In all cores the majority of the algae occurred in the upper 0–1·5 cm. layer and rapidly decreased in number with increasing depth (Table I). No seasonal variation in the pattern of distribution was apparent, although ideally more cores should have been taken to confirm this. The pattern of distribution was similar in the two moss species but higher total numbers of algae were detected in *Polytrichum* than in *Chorisodontium*.

TABLE I. THE VERTICAL DISTRIBUTION OF ALGAE IN DEEP CORES

Vegetation type	*Date*	*Percentage frequency at each depth** (cm.)						*Total number of algae in core* ($\times 10^3$ cm.$^{-2}$)
		0–1·5	1·5–3·0	3·0–4·5	4·5–6·0	6·0–7·5	7·5–9·0	
Polytrichum–Chorisodontium	August 1972	92·6	5·7	1·1	0·4	0·2	–	459
Polytrichum	March 1973	96·0	3·4	0·4	0·2	–	–	2,057
Chorisodontium	March 1973	93·0	3·6	2·3	1·1	–	–	257
Polytrichum	January 1974	99·0	0·5	0·2	0·1	0·1	0·02	10,276
Chorisodontium	January 1974	72·7	14·6	5·2	3·0	0·4	4·1	267

* Data are from single cores at each sampling occasion.

In the upper layers of the moss and peat.

i. *Thin slicing of cores.* The number of colonies derived from algae transferred from each exposed core surface to the surface of the agar plate varied from nil to a maximum of 300 at 12 mm. depth in one core. Counts of over 100 colonies were accurate only to the nearest ten colonies, since above this number the amount of confluent colony growth increased. The pattern of distribution was similar for all five cores with low numbers of algae towards the apices of the moss shoots rapidly increasing to a maximum between 8 and 14 mm. and then declining rapidly in the lower parts of the cores (Table II).

ii. *Direct observation of algae on moss.* Most algae occurred as small gelatinous colonies usually containing from four to ten cells adhering to the leaf surfaces. Other cells, which ranged in shape from spherical to ellipsoidal or almost cylindrical, were single and free or in small loose micro-colonies. All cells observed contained green or yellow-green chromatophores. Internal cell structure was often impossible to ascertain because of the presence of large quantities of oil globules and few algae could be identified. Few *Monodus subterraneus* cells were noted, possibly because of their small size and pale colour. Table III gives the mean numbers of algae on 20 *Chorisodontium* leaves ranging from 5·4 to 7·2 mm. in length. 90·8 per cent of all cells counted occurred between 0 and 2·1 mm. from the leaf bases with maximum numbers between 0·6 and 1·2 mm. The remaining 9·2 per cent were between 2·1 mm. from the leaf bases and the leaf apices.

iii. *Culture of algae from individual moss leaves.* The numbers of algae cultured from every second or third healthy *Chorisodontium* leaf are presented in Table IV. The uppermost leaves bore few algae. Numbers increased progressively down the shoots with most algae on the seventh and eighth leaves examined, at a distance of 7–10 mm. from the shoot apices. The results for *Polytrichum* followed a similar trend (Table V). The lower brown *Polytrichum* leaves from a distance of 4–8 mm. from the shoot apices had considerably higher counts. The portions of *Cephaloziella varians* shoots produced an average count of 42 ± 9, similar to the numbers on the lower *Chorisodontium* leaves.

Seasonal changes in algal numbers

Regular counts. The mean counts for the 0–1·5 cm. part of the six cores from each moss over the 15 month sampling period are shown in Fig. 1. The mean numbers of algae in

TABLE II. THE VERTICAL MICRO-DISTRIBUTION OF ALGAE IN MIXED *Polytrichum–Chorisodontium* CORES

Depth down core (mm.)	*Mean number of algal colonies, with standard error, from each exposed 1·4 cm.² core surface**		*Algal colonies as percentage of total from core*	
0	0·0	±0	0	
2	6·4	±1·9	1·3	
4	14·0	±3·8	3·2	
6	43·0	±18·2	9·0	
8	67·4	±15·1	14·5	
10	134·2	±22·1	26·5	77·6
12	126·4	±46·8	24·3	
14	61·2	±23·2	12·3	
16	14·2	±4·1	3·3	
18	6·4	±2·3	1·5	
20	4·0	±0·5	0·9	
22	2·0	±0·7	0·4	
24	1·4	±0·2	0·2	
26	1·4	±0·7	0·2	
28	1·4	±0·5	0·2	
30	1·2	±0·5	0·2	
32–46	7·2	±0·6	1·5	

* Data are means of five cores.

TABLE III. NUMBERS OF ALGAL CELLS ON CONSECUTIVE SECTIONS OF *Chorisodontium* LEAVES

Distance from base of leaf (mm.)	*Mean number of algal cells per leaf section, with standard error**		*Algal colonies as percentage of total leaves*	
Leaf base–0·3	3·0	±0·9	7·6	
0·3–0·6	4·0	±1·3	10·1	
0·6–0·9	8·5	±2·0	21·4	
0·9–1·2	7·0	±1·4	17·6	
1·2–1·5	4·0	±1·2	10·1	
1·5–1·8	4·2	±1·5	10·6	
1·8–2·1	5·3	±3·2	13·4	
2·1–2·4	0·6	±0·4		
2·4–2·7	0·3	±0·15	9·2	
2·7–3·0	0·4	±0·15		
3·0–leaf tip (5·4–7·2)	4·5	±1·6		

* Data are means of 20 leaves.

TABLE IV. NUMBERS OF ALGAE ON CONSECUTIVE *Chorisodontium* LEAVES

*Leaf**	*Mean number of algal colonies per leaf, with standard error†*		*Algal colonies as percentage of total on consecutive leaves*
1 Terminal leaf	1·1	±0·5	0·9
2	0·9	±0·4	0·9
3	3·6	±1·2	3·4
4	7·7	±2·7	5·9
5	11·5	±2·7	9·4
6	14·9	±4·0	12·8
7	41·3	±14·8	35·0
8 Lowest green leaf	37·3	±6·0	31·7

* The numbers refer to the leaves sampled; one or two leaves were left between each leaf which was removed.
† The data are means of ten plants.

TABLE V. NUMBERS OF ALGAE ON CONSECUTIVE *Polytrichum* LEAVES

*Leaf**	*Mean number of algal colonies per leaf, with standard error†*		*Algal colonies as percentage of total on consecutive leaves*
1 Terminal leaf	4·4	±1·2	<1
2	9·0	±1·3	<1
3	14·8	±2·5	1
4	27·3	±6·9	2
5	63·0	±10·3	4
6 Lowest green leaf	87·3	±10·6	5
7 Brown leaf	1,408·0	±288·0	86

* Although every leaf was sampled, the numbers refer to every second or third leaf for which data are presented.
† The data for leaves 1–6 are means of six plants. The data for leaf 7 are the mean of 25 leaves, five from each of five plants.

Chorisodontium were lower than those in *Polytrichum* on all sampling occasions. Although numbers fluctuated throughout the period, no significant changes were detected in either moss; there was neither a summer increase nor a winter decrease. These fluctuations are probably due to sampling and counting errors and to the low number of cores examined on each sampling occasion. However, it is considered that any significant change in the numbers of algae would have been detected if it occurred.

Since no seasonal changes were detected, the counts of all samples can be considered together and comparisons can be made between the numbers of algae in areas A and B and in the two moss species (Table VI). At the 90 per cent level of confidence, the counts in *Polytrichum* in areas A and B are significantly greater than those in *Chorisodontium*; the count in *Chorisodontium* is significantly greater in area B than in area A, while the count in *Polytrichum* is not significantly different between the areas.

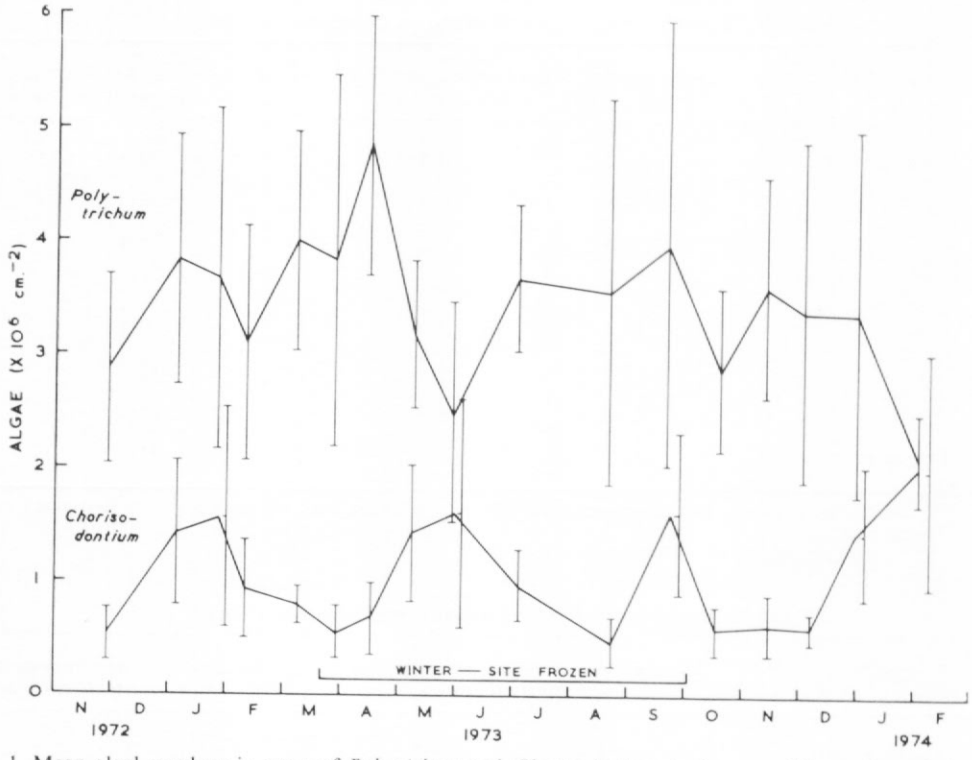

Fig. 1. Mean algal numbers in cores of *Polytrichum* and *Chorisodontium* turf over a 15 month period, with standard errors (means of six cores).

TABLE VI. NUMBERS OF ALGAE IN *Polytrichum* AND *Chorisodontium*, FROM AREAS A AND B, OVER A 15 month SAMPLING PERIOD

Moss	*Mean number of algae, with standard error** ($\times 10^3$ cm.$^{-2}$)		
	A	*B*	*Mean*
Polytrichum	3,639 ± 328	3,364 ± 368	3,439 ± 156
Chorisodontium	755 ± 189	1,331 ± 219	1,046 ± 119

* Data are means of 50 cores.

During the 15 month sampling period, 2,805 algal colonies, randomly selected from the culture plates, were examined microscopically and the algae identified. Table VII gives the total numbers of colonies of certain species in each moss in the two summer periods (November 1972–March 1973 and October 1973–February 1974) and in the winter (March 1973–October 1973). *M. subterraneus* predominated throughout all samples and accounted for over 88 per cent of the total. There were neither significant seasonal differences nor differences between the two moss species in the proportions of the different species of algae recovered. No differences between sampling areas A and B were apparent in the data and no distinction is made between these areas in Table VII.

Algal re-colonization of a cleared area of moss. The mean number of algae per cm.^{2} is shown in Table VIII together with the percentage frequency of the algae identified from

TABLE VII. THE PROPORTIONS OF DIFFERENT ALGAE IN *Polytrichum* AND *Chorisodontium* IN SUMMER AND WINTER

Species of algae	*Total numbers of colonies randomly removed from dilution culture plates*					
	Polytrichum			*Chorisodontium*		
	Summer 1972–73	Winter 1973	Summer 1973–74	Summer 1972–73	Winter 1973	Summer 1973–74
Monodus subterraneus	468	451	480	415	360	456
Radiococcaceae B	9	5	4	9	7	6
Chloromonas sp.	5	2	0	5	6	0
Gongrosira terricola	0	0	3	10	10	10
Other algae	7	3	24	11	4	35

TABLE VIII. NUMBERS OF ALGAE WHICH RE-COLONIZED AN AREA CLEARED OF LIVING MOSS

Sampling dates	*Mean number of algae with standard error** ($\times 10^3$ cm.$^{-2}$)	*Number of colonies examined for identification*	*Percentage frequency*		
			Monodus subterraneus	*Chloromonas* sp.	*Other algae*
20 November 1973	12 ± 9	50	90	0	10
5 December 1973	11 ± 12	50	74	2	24
28 December 1973	87 ± 17	100	41	54	5
25 January 1974	223 ± 45	97	52	37	11
21 February 1974	367 ± 79	100	43	40	17
11 March 1974	845 ± 367	100	57	33	10

* Data are mean of ten cores.

random colonies taken from the plate counts. Algal numbers were low until about mid-December when they began to increase rapidly; by the onset of winter numbers were very high, there having been a 70-fold increase during the season. An initially high frequency of *M. subterraneus* soon dropped to a fairly constant level of around 50 per cent of the total. This decline was accompanied, in late December, by a rapid increase in *Chloromonas* sp. which then remained around 35 per cent of the total algal population, a considerably higher percentage than obtained in the counts in the two mosses over the 15 month sampling period.

Observations on slides buried in peat. M. subterraneus, *Chloromonas* sp. and Radiococcaceae B were recorded on the slides removed within 3 hr. of their introduction into the moss and peat. Other unidentifiable green and yellow-green unicells and gelatinous colonies were noted but the cell contents were either disorganized or masked by food storage material. The *M. subterraneus* cells were mostly single, although some occurred in loose aggregates of less than four or five. Some were in the process of autosporulation, forming two spores. Most of the gelatinous colonies contained less than ten cells and only one was seen with *c.* 100 cells.

Two changes had occurred by the time of the second removal of slides 4 months later. There were far more *M. subterraneus* cells adhering to the slides and most of these were in small

compact micro-colonies of up to 14 cells. The gelatinous colonies had also shown a significant increase in size; some were very large and contained *c.* 1,000 cells. However, most consisted of *c.* 50 cells. It was apparent that algal growth had occurred on the slides over the summer.

Horizontal distribution of the algae

Culture counts. The results of the counts are presented in Table IX together with the identification of the algae from samples c–g.

The data may be summarized as follows:

i. The results presented earlier showed that *Polytrichum* harboured significantly more algae than *Chorisodontium* over a 15 month sampling period. This was confirmed over a wide area of the site. The numbers of algae in the bare eroded peat were similar to those in the living *Polytrichum*.

ii. There was no significant difference between the numbers of algae in densely or loosely packed *Polytrichum* shoots or in the areas of bare peat. The numbers were typical of those obtained previously for *Polytrichum*.

iii. On both sampling occasions the moribund moss gave a significantly higher count than the healthy moss. The latter counts resembled those of *Chorisodontium* in (i). In November no living moss apices were visible at the surface of the moribund moss. By the second sampling occasion, however, several of the plants had produced new shoots mostly from lateral buds a few millimetres down the stem. The proportion of *M. subterraneus* was low when compared with the samples over the 15 month period, and *Stichococcus bacillaris* was high.

iv. Five of the six pairs of cores produced a higher count in the exposed bare peat than in the sheltered moss of the rippled turf. *M. subterraneus* was again the dominant alga.

v. There was no difference between the two sample types. Despite the higher mean count in the lichen-free than in the lichen-covered moss the variation was too great for the difference to be significant.

vi. The bare eroded peat along the bottom edge of the moss banks had the highest numbers of algae recorded for any terrestrial site investigated on Signy Island (author's unpublished data); in contrast, the overlying *Chorisodontium* gave typically low counts. The highest count from a single core of eroded peat was $38 \cdot 4 \times 10^6$ algae per cm.^{2}. When peat with a visibly green surface of algae was chosen, the mean count was higher. In both of the bare peat samples *M. subterraneus* was dominant but the *Chorisodontium* samples were unusual in having a high frequency of a species of Pleurochloridaceae.

vii. The influence of the temporary melt rivulet was different in the two moss types. In *Polytrichum*, all six cores within the rivulet produced higher counts than those taken beyond. The algal flora was unusual in containing a low proportion of *M. subterraneus* and many *Ellipsoidion* cf. *perminimum* cells. In *Chorisodontium*, there was a typically high proportion of *M. subterraneus* and the count was lower in the moss within the melt in five of the six pairs of cores. There was no significant increase in algal numbers in *Chorisodontium* from within the area over which water had flowed on the second sampling occasion, 2 months later, long after the rivulet had ceased to flow.

Observations on macroscopic algae. Pale green, firmly gelatinous algal colonies occurred in the damper areas of the site. They were irregularly shaped three-dimensional masses, rarely more than 2 cm. across. They were not seen amongst the healthy shoots of the two mosses but occurred on the surface and embedded in the upper layers of the bare eroded peat, particularly where it was shaded and damp, as along the eroded edges of the banks and in cracks in the peat surface.

Culturing such growths revealed that the major algae present were two gelatinous species (A and B) of Radiococcaceae. *M. subterraneus*, *S. bacillaris* and Pleurochloridaceae, which were not seen during direct microscopic observation of the colonies, but which were probably present in low numbers, also appeared. In culture these gelatinous forms rarely had stratifications in the mucilage (Broady, 1977*b*) but in those observed in field material the stratifications were often distinct.

TABLE IX. THE HORIZONTAL DISTRIBUTION OF ALGAE IN THE UPPER 1·5 cm. IN VARIOUS VEGETATION COVER

Sampling sites	*Sampling dates*	*Mean number of algae, with standard error** ($\times 10^3$ cm.$^{-2}$)	*Number of colonies examined for identification*	*Percentage frequency*			
				Monodus subterraneus	*Pleurochloridaceae*	*Ellipsoidion* cf. *perminimum*	*Other algae*
a. *Polytrichum*	October 1972	1,680 ± 1,048	–	–	–	–	–
Chorisodontium	October 1972	139 ± 93	–	–	–	–	–
Bare peat	October 1972	1,390 ± 625	–	–	–	–	–
b. Dense *Polytrichum*	November 1973	2,970 ± 2,539	–	–	–	–	–
Loose *Polytrichum*	November 1973	4,960 ± 4,106	–	–	–	–	–
Bare peat	November 1973	3,660 ± 3,671	–	–	–	–	–
c. Healthy *Polytrichum* (1)	November 1973	222 ± 91	50	58	12	0	30
Moribund *Polytrichum* (1)	November 1973	4,142 ± 3,954	50	74	4	0	22
Healthy *Polytrichum* (2)	January 1974	134 ± 68	–	–	–	–	–
Moribund *Polytrichum* (2)	January 1974	4,087 ± 1,970	–	–	–	–	–
d. Exposed side of moss ridge, bare peat	November 1973	951 ± 177	50	88	10	0	2
Sheltered side of moss ridge, live *Chorisodontium*	November 1973	385 ± 548	50	84	2	0	14
e. Lichen-covered *Chorisodontium*	November 1973	523 ± 276	50	84	12	0	4
Lichen free *Chorisodontium*	November 1973	1,495 ± 973	50	94	4	0	2
f. *Chorisodontium*	November 1973	463 ± 262	100	47	51	0	2
Bare peat	November 1973	17,240 ± 10,758	50	94	4	0	2
Bare peat visibly covered by green algae	December 1973	22,438 ± 4,886	50	80	4	4	12
g. *Polytrichum* in temporary melt stream	November 1973	8,472 ± 5,287	109	12	7	61	20
Polytrichum in adjacent dry area	November 1973	2,305 ± 1,270	121	63	3	24	10
Chorisodontium in temporary melt stream (1)	November 1973	139 ± 89	50	96	0	0	4
Chorisodontium in adjacent dry area (1)	November 1973	335 ± 153	50	96	0	0	4
Chorisodontium in temporary melt stream (2)	January 1974	166 ± 120	–	–	–	–	–
Chorisodontium in adjacent dry area (2)	January 1974	687 ± 500	–	–	–	–	–

* The data are means of five cores (a and c), four cores (b) and six cores (d, e, f and g).

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Other aspects of algal ecology

Interactions of the algae with other members of the micro-flora. Microscopic examination of slides removed from the site proved to be the most useful technique for revealing associations between algae and fungi or bacteria. The gelatinous algal colonies, in particular, were often thickly covered with interwoven epiphytic growths of sterile septate and aseptate fungal hyphae which were hyaline or melanized. Most growth was over the surface of the mucilage and the hyphae were not seen to penetrate algae. There was often considerable bacterial growth within and on the surfaces of the colonies.

The frequent cells of *M. subterraneus* which occurred singly or in small aggregates on the slide surfaces were also seen in loose associations with fungal hyphae, yeast cells and bacteria. Fig. 2a shows a small *M. subterraneus* colony which contained yeast cells amongst the algae. Several fungal hyphae passed between the algae and one hypha extended to another smaller colony of algae. Most aggregates of algae had associated bacteria (Fig. 2b). Some algae were ruptured and were observed releasing their cell contents. *M. subterraneus* and a fungus with fine, hyaline aseptate hyphae formed a more advanced form of association approaching a semi-lichenized state. This is illustrated in Fig. 2c where the different stages in the formation

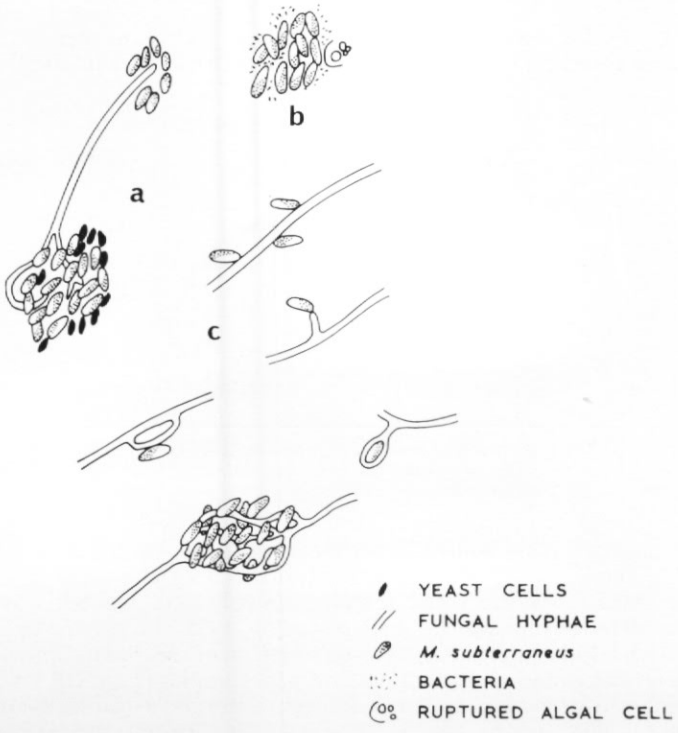

Fig. 2. Associations between algae and the heterotrophic micro-flora.

of the association are shown. Several cells lay against the fungal hyphae and occasionally stimulated branch formation; sometimes the hypha would produce an anastomosing loop passing close to the algal cell. At a later stage the fungal hyphae encircled the algal cell but no penetration was seen. Where a group of algal cells occurred close together, the fungal hyphae branched and anastomosed round these forming an interweaving mesh. Such associations between fungi and algae developed within a single summer, appearing on slides buried in the moss for this short period.

Algae as a food source for soil invertebrates. Information on the Protozoa was limited to microscopic observation of naked Amoebae and ciliates containing green algal unicells. Both were seen in moist enrichment cultures. The collembolan, *Cryptopygus antarcticus*, was more intensively studied. The results presented here summarize more extensive unpublished data.

Direct observation of guts showed algal cells to be present but they were never the dominant gut content, fungal hyphae being more abundant. The most frequently seen algae were the gelatinous colonies; a proportion of the cells would often be ruptured but the gelatinous matrices remained intact. *M. subterraneus* and other single, but unidentified, green and yellow-green cells were observed, as well as empty and ruptured cell walls. Occasionally the green cell contents were seen spilling out of the ruptured cells. Similarly, microscopic examination of faecal pellets revealed that fungal hyphae were dominant and algal cells only infrequently present. Many of the algae had healthy green contents even after passage through the guts. The presence of viable algae was confirmed when colonies of *M. subterraneus* and Radiococcaceae B were cultured from both guts and faeces on BBM agar plates. From 42 faecal pellets spread over nutrient agar plates, microbial growth was apparent in 35; 23 of these produced algae. When cultured colonies of Radiococcaceae B were presented to *C. antarcticus* the animals fed on the alga. The guts were full of algal cells and faeces contained both ruptured and empty cells and cells with apparently healthy green contents.

Losses of algae in snow melt water. The numbers of algae per ml. of melt water are shown in Table X. There was little difference in mean numbers between sampling times, although

TABLE X. NUMBERS OF ALGAE IN SNOW MELT WATER

Sampling dates	*Mean number of algae, with standard error** (ml. melt water^{-1})
November 1972	394 ± 49
October 1973	263 ± 49
November 1973	221 ± 60

* Data are mean of seven (1972) and ten (1973) samples. A replicate of >9,000 ml.$^{-1}$ has been omitted from the 1972 count.

individual replicates ranged from 86 to 673 per ml., except for one count of over 9,000 per ml. in November 1972. The data showed no correlation between the number of algae and the distance down the slope from which the sample was collected. Neither was any significant change in numbers detected during the melt period in 1973. 14 species of Xanthophyceae, Euchlorophyceae and Ulothricophyceae were recorded, with *M. subterraneus* being the most abundant. Six species not found in other moss and peat samples from SIRS 1 appeared on the culture plates, namely *Gloeobotrys terrestris* Reisigl, *Chloridella* sp. A, *Chlorococcum humicolum* (Naeg.) Rabh., *Botrydiopsis* sp., *Myrmecia bisecta* Reisigl and *Stichococcus minutus* Grintzesco and Peterfi. It is probable that these had been washed from different vegetation nearby.

DISCUSSION

The predominance of *M. subterraneus* (Table VII) agrees with the findings of Miller and Fogg (1957), who studied the physiology of this alga in pure culture. They found maximum growth in a medium with a low concentration of calcium or a high monovalent to divalent cation ratio, and that there was a low tolerance to phosphate. Suitable nutrient conditions would be expected in the acid *Polytrichum–Chorisodontium* turf, and Allen and others (1967) have shown that low concentrations of calcium and phosphorus occur in such Signy Island

vegetation. The absence or low abundance of diatoms and Cyanophyceae is not unusual for acid sites (John, 1942; Lund, 1945, 1947).

The occurrence of the large numbers of algae at or close to the soil surface is a well-known phenomenon (Lund, 1967). In the SIRS 1 moss turf, most algae occurred in the 0–1·5 cm. layer where light levels are sufficient for their autotrophic growth (Table I). It is considered unlikely that this pattern would change during the year as the one winter core had a similar distribution of algae to the four summer cores. However, algae also occur deeper in the soil below the level to which light could penetrate. Petersen (1935) attributed their vertical transport to these lower parts to rain and earthworms. On Signy Island, however, earthworms are absent and the largest soil animal, the collembolan *Cryptopygus antarcticus*, is only *c.* 2 mm. long and occurs mostly in the 0–3 cm. zone. It is unlikely that this animal would transport cells down to 7·5 and 9·0 cm. The frequent summer precipitation is rapidly absorbed into the spongy peat and unattached algal cells may be carried down with the water. The upward growth of the moss would also place the algae at a progressively greater distance from the moss apices. Each summer *Polytrichum alpestre* shoots extend apically by 2–5 mm. (Longton, 1970) and exceptionally by over 10 mm. (Smith, 1972). Algae, originally near the surface of the peat, are gradually positioned lower down the profile if they are not re-distributed on to the new upper moss shoots. A proportion of these cells may be resistant and survive for long periods. Deeper light penetration down cracks and fissures in the peat may also contribute to localized growths of algae well below their normal depth.

Within the top 1·5 cm. the algae are most abundant between 8 and 14 mm. (Table II). The low numbers found in the upper 8 mm. are due to a combination of factors. The current year's growth increment is largely uncolonized by algae; the micro-climate at the level of the moss apices is more severe than that a few millimetres within the moss (Longton, 1972); evaporation stress at the moss apices is considerable and the amount of free water available would be small except at times of precipitation. Also, algae in the apical region of the moss shoots will probably be washed down into the lower parts by rain and melting snow.

Below 14 mm., although adequate moisture is present, the light levels are low due to shading by the moss above, and algal numbers are greatly reduced. Longton (1970) stated that *Polytrichum alpestre* absorbs a high proportion of the incoming radiation within a layer only a few millimetres below the stem apices.

Between 8 and 14 mm. conditions are optimal for the production of a large population of algae. Light still penetrates to this depth and adequate moisture is held in the capillary spaces between the densely packed moss leaves and shoots. The temperature on sunny days of high insolation may rise well above the ambient air temperature and may reach 30° C at a depth of 15 mm. (unpublished micro-climate data). In such conditions, rapid growth of the algae would be expected.

The low numbers of algae at the shoot apices are emphasized by the culture counts on the individual leaves and the microscopic examination of *Chorisodontium* leaves (Tables III–V). Colonization of the leaves of both moss species appears to be rare; few cells are deposited on their surfaces and the exposed apices of the *Chorisodontium* leaves also have low algal numbers. Only the flagellate cells of *Chloromonas* sp. and the zoospores of *Gongrosira terricola* would be able to distribute themselves in a film of water. However, the general absence of free water at the apices of the moss shoots would restrict the usefulness of this means of distribution. The large majority of the algae in SIRS 1 are non-motile and would have to depend on external means for their deposition on new moss leaves and shoots. There are three possible dispersal agents. Water brought by capillary action from deeper in the peat (Gimingham and Smith, 1971) could dislodge algal cells and move them higher up the profile. Soil invertebrates may carry cells adhering to their bodies and deposit them on the upper leaves. Collembolan faeces containing viable algae may be deposited on to the new moss growth. Lateral shoots are initiated deeper within the peat (Longton, 1970) and these grow through the zone of high algal numbers. They could transport algae upwards to the surface of the moss turf.

Throughout the two summer sampling periods no increases in algal numbers were detected in either moss (Fig. 1). The standing crop remained the same and losses of algae from the site were equivalent to the production. That production of algae does occur in summer was confirmed both by the re-colonization experiment and the observation of slides buried in the peat.

In both, large increases in algal numbers were detected during one summer. However, in these experiments the algae were not competing with growing moss. In stands of growing moss a proportion of the cells are re-distributed on to the new moss leaves and it is the rapid reproduction of these algae, probably at a rate similar to that detected in the re-colonization experiment (Table VIII), which compensates for the large numbers lost by shading and so maintains a constant standing crop.

Other mechanisms may cause algal deaths but these are considered to be less important than the shading effect. Precipitation could wash algae down the profile, and at the time of the spring melt a proportion of the algal population is washed out of the site in melt water but in insufficient quantity to produce a detectable decline in the numbers. Where temporary melt streams flow over *Chorisodontium*, algal numbers are lower than in adjacent dry moss. However, in *Polytrichum* no such relationship was found and numbers were in fact higher within the stream, possibly due to stimulated growth of *Ellipsoidion* cf. *perminimum* by the wet conditions (Table IX). The densely interwoven tomentum of rhizoids of *P. alpestre* may prevent algae from being washed away. Although Protozoa and Collembola graze on algae, their effects on the population are believed to be small since the ingestion of algal cells was infrequently observed. In summer, the temperature of the upper layers of the moss frequently falls below 0° C during the night. The freezing and thawing of cells may cause rupture and death, but during the 7 month winter when the site was constantly frozen, there was no decline in algal numbers and they are apparently tolerant of a long period of freezing.

The regular counts revealed a significantly greater number of algae in *Polytrichum* than in *Chorisodontium* (Table VI), although similar algae were present in both with *Monodus subterraneus* predominating in the plate counts (Table VII). This may be related to the greater ability of the latter moss to transmit water, which arrives at the apices, down the stems and into the lower peat (Gimingham and Smith, 1971). More algal cells may be washed down in this moss resulting in the lower population in the 0–1·5 cm. zone. In sampling area B, where the counts in *Chorisodontium* were significantly higher than in the same moss from area A, the area covered by pure *Chorisodontium* was lower than in area A and the peat below the *Chorisodontium* often resembled the more closely matted peat below *Polytrichum*. It is likely that *Polytrichum* once predominated before being colonized by *Chorisodontium*, a feature common in the establishment of the latter moss (Smith, 1972), and the washing of cells down the profile may be made more difficult by the densely interwoven underlying peat remaining from the previous more extensive *Polytrichum* cover.

Although no differences were noted in algal numbers in the different densities of *Polytrichum* growth (Table IX, sample b) in November 1973, there were significant differences between healthy and moribund *Polytrichum* shoots (sample c). In the moribund moss the algae built up a large population because of the absence of apical moss growth and the lack of shading. In the healthy *Polytrichum* there had been good growth of the moss and thus some degree of shading of algae lower down the stems. The mean count here was considerably lower than the mean in this moss species over the 15 month sampling period, and it is possible that particularly rapid growth of the healthy *Polytrichum* of sample c had not allowed algal numbers to build up to such an extent. In the second sample of the moribund *Polytrichum*, at the end of the summer, it was noted that there were healthy moss apices at the surface of the turf. These had been produced from lateral buds a few millimetres down the stems. If these continued growing in the following season, it is probable that the numbers of algae would fall due to renewed shading of the algae and the necessity of colonizing the new moss.

Numerically, the algae appear to be more important than bacteria and fungi in the upper moss and peat. Baker (1970) obtained only $0{\cdot}3\times10^6$ bacteria per g. dry weight of peat and 1×10^6 yeasts per g. dry weight in the 1–2 cm. zone of a *Chorisodontium* moss bank on Signy Island. The algal counts are *c.* 12×10^6 per g. dry weight in the *Polytrichum* and $3{\cdot}5\times10^6$ per g. dry weight in *Chorisodontium*. A. D. Bailey (unpublished data), in a moss bank similar to SIRS 1, obtained a culture count of $0{\cdot}18\times10^6$ fungi and $0{\cdot}2\times10^6$ bacteria per $cm.^3$ of peat from a depth of 1·3 cm., both considerably lower than the present culture counts of algae.

The relative importance of the different algae in the site is not accurately conveyed by the plate counts. Although considerably more colonies of *Monodus subterraneus* than the gelatinous form Radiococcaceae B appeared on the culture plates (Table VII), the importance of the

latter is probably underestimated. Each colony of *M. subterraneus* is the product of a single cell in the innoculum as these free unicells are probably thoroughly distributed by the homogenization treatment. Measurements of cells from culture gave a mean volume of *c.* 40 μm.^{3} for *M. subterraneus* cells. However, microscopic observation of sample homogenates showed that the gelatinous colonies are not separated into individual cells. Each colony contained a mean of about five cells and, including the mucilage, approximated a sphere 56 μm. in diameter with a volume of *c.* 92,000 μm.^{3}. Each gelatinous colony appearing on a culture plate may be assumed to have developed from an initial propagule of this size in the innoculum. Thus, each gelatinous colony in the count would be 2,300 times more important than a colony of *M. subterraneus*, in terms of the volume and hence the biomass, than the propagule producing such a colony. Over the 15 month sampling period a total of 2,630 colonies of *M. subterraneus* was removed from the culture plates, compared with only 40 colonies of the gelatinous Radiococcaceae B (Table VII). However, from the above considerations it can be seen that the gelatinous forms would contribute 35 times $\left(\frac{40 \text{ colonies} \times 92{,}000\,\mu\text{m.}^3}{2{,}630 \text{ colonies} \times 40\,\mu\text{m.}^3}\right)$ more algal volume and biomass than *M. subterraneus*.

Shtina and Nekrasova (1971) stated that the most essential function of algae is their importance as a diet for heterotrophic micro-organisms. They described an "algosphere" in which bacteria are the permanent satellites of algal cells. This phenomenon was seen in SIRS 1, where bacteria associated with *M. subterraneus* and gelatinous algal micro-colonies on the glass slides. The mucilage of Radiococcaceae B could be particularly important as a food source. Yeast cells and fungal hyphae also form part of the "algosphere" (Fig. 2). The association in which fungi produced branched growths of hyphae around the cells of *M. subterraneus* may be an attempt by the fungus to obtain secreted algal products. A relationship with a similar morphology has been reported by Jaag (1933) in which a species of *Coccomyxa* and moss rhizoids are loosely combined. However, no such association was seen in the present study. It appears that the heterotrophic microbial components are partially supported by the algae, either by organic products secreted from living cells or by the utilization of cell contents of dead cells. Stimulation of the heterotrophic micro-flora by the algae may enhance their ability to decay moss tissue.

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