THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: IX. THE ECOLOGY OF THE ALGAE OF SITE 2, A MOSS CARPET

By P. A. Broady

Abstract. The population dynamics of 40 species of algae were followed over a 21 month period at a moss-carpet site (SIRS 2). The vertical distribution, both in deep cores and in the upper 1·5 cm. of the carpet, was examined. Direct microscopic observation of individual moss plants showed differences in the vertical micro-distribution of different species of algae, of which that of *Nostoc muscorum* Kuetz. was particularly interesting. Qualitative and quantitative variations in the horizontal distribution of the algal flora 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, particularly to the moisture regime of the habitat. The importance of the algae in relation to the general ecology of the ecosystem is discussed.

This paper describes the ecology of the algae at the Signy Island terrestrial reference site (SIRS) 2, a swamp community consisting predominantly of the carpet-forming mosses *Calliergon sarmentosum*, *Calliergidium austro-stramineum* and *Drepanocladus uncinatus*, and the foliose liverwort *Cephaloziella varians*. The site has been described in some detail by Tilbrook (1973). The ecology of the algae of the contrasting moss-turf site (SIRS 1) has been described by Broady (1977) and, where possible, the format of the present paper follows that of the latter work to facilitate comparisons between the two sites.

Methods

Identification of the algae

Direct microscopic examination and culture techniques were used as described by Broady (1977, in press).

Vertical distribution of the algae

In deep cores. Two cores, each 1·5 cm. in diameter, were removed, one in July 1972 and one in June 1973. The sampling and the counting techniques were identical to those used on SIRS 1 (Broady, 1977). It is a well-known phenomenon that the large majority of algae occur in the top layers of the soil and vegetation, and the sampling and analysis of single cores in each winter was intended merely to confirm such distribution in Antarctic ecosystems. It is appreciated that many samples would have been required if the data are to be statistically valid.

In the upper layers of the bryophytes. All the data were obtained by the direct microscopic examination of moss and liverwort shoots. Single cores were sampled at monthly intervals between September 1973 and March 1974 from various parts of the site. The samples were removed using a corer of 1·5 cm. diameter and they were transported to the laboratory with as little disturbance as possible, They were examined soon after collection, usually within 24 hr., and until then were kept in the dark at field temperature. Individual bryophyte shoots were dissected from the cores and the positions and numbers of algae were counted in successive 0·5 mm. lengths of the plants. Algae were recorded on a total of 88 moss and liverwort shoots isolated from 15 cores. The depth to which the moss and liverwort tissue remained green was also noted for each shoot.

Seasonal changes in algal numbers

Three areas, designated A, B and C, were chosen for sampling. Each area consisted of a strip 5 m. by 1 m. within the original transects comprising 150 1 m. squares marked out

when the site was established (Tilbrook, 1973). The vegetation within each area comprised almost entirely *Calliergon* interspersed with occasional patches of *Calliergidium*, *Drepanocladus* and *Cephaloziella*.

Sampling was carried out at approximately monthly intervals when a single sample was taken from each area. In summer the corers were simple aluminium cylinders with sharpened ends and a cross-section of 10 cm.^{2}; a separate corer was used for each sample. To prevent water loss from the saturated cores, a rubber stopper was inserted into the bottom of the cylinder immediately after coring. The corer was then placed upright in a sterile, screw-capped aluminium cannister and transported to the laboratory. In winter a power-driven corer (see Broady, 1977) was used, since the site was frozen.

The upper 1·5 cm. of each core was homogenized at 14,000 r.p.m. in 100 ml. of sterile water for 2 min. The homogenate was diluted initially by × 10 followed by eight serial × 4 dilutions.

Three counting techniques were employed:

i. Direct microscopic count. 10 ml. from the homogenate of each core were bulked and, after thoroughly shaking by hand, one drop was transferred to the counting chamber of a 0·1 mm. deep haemocytometer slide. All algal cells and filaments were counted in five random traverses across the slide at a magnification of × 400. Five aliquots of bulked homogenates were counted for each sample.

ii. Plate-culture count. The method was identical to that used for SIRS 1 (Broady, 1977) except that the dilutions plated were the initial × 10 and the following two serial × 4 dilutions. Two media were used, Bold's modified Bristol's medium (BBM) (Chantanachat and Bold, 1962) and BBM supplemented with actidione at 100 μg. ml.$^{-1}$, the latter allowing only the growth of the Cyanophyceae. The plates were incubated at laboratory temperature (*c.* 18° C) for 3 weeks, under constant illumination supplied by four 30 W daylight fluorescent tubes.

iii. Most probable number count (m.p.n.). Each of the nine dilutions was used to inoculate 25 ml. test tubes containing 10 ml. of either BBM or BBM+actidione. For each core treated, five tubes of each medium were inoculated with 0·5 ml. of the × 10 dilution and eight groups of ten tubes of each medium with 0·5 ml. of each of the eight serial × 4 dilutions. Incubation was as for the plate count but on one occasion the BBM+actidione tubes were left to incubate for 10 weeks. The developing algal growths were removed for microscopic examination and as many as possible were identified. From the total number of tubes showing algal growth the number of algae present in the initial inoculum was calculated using statistical tables (Fisher and Yates, 1963).

Horizontal distribution of the algae

The following counts and observations were performed:

i. To examine the variation within and between areas A, B and C four 1·5 cm.^{2} cores were randomly removed from each area in January 1974. A plate count using BBM agar was performed on each core; 50 colonies were removed randomly from each dilution plate and these were microscopically examined and identified in order to ascertain the proportions of the different algae in each area. For comparison, six random cores were removed in February 1974 from an area of *c.* 5 m.^{2}, designated area D, towards the eastern edge of the site where the turf-forming *Chorisodontium aciphyllum* was invading the *Calliergon*-dominated carpet. Each core consisted of *c.* 50 per cent of each moss. Plate counts were performed on each core and 50 random colonies were identified.

ii. A direct microscope count was performed on the homogenate of six bulked 1·5 cm.^{2} cores randomly removed in February 1974 from each of two *c.* 1 m.^{2} areas, designated

E and F, of pure *Cephaloziella varians*. Area E was immediately adjacent to a small permanent melt pool and area F was in a typically boggy part of the site but not adjacent to standing water.

iii. Observations were made on the distribution of macroscopic green, gelatinous algal colonies which were locally distributed on the site.

Other aspects of algal ecology

Interactions of algae with other members of the micro-flora. Notes and drawings were made of the interactions between algae and the fungi and bacteria during direct microscopic observation of freshly collected material, particularly during the investigation of the vertical micro-distribution of the algae. Microscope slides embedded in the top few centimetres of the peat in November 1972, in a similar manner to those in SIRS 1 (Broady, 1977), were examined microscopically at intervals during the following summer (December–March).

Algae as a food source for soil invertebrates. Microscopic examination and culture was performed on the guts and faeces of the collembolan *Cryptopygus antarcticus*. Notes were also made on the Protozoa, Rotifera and Tardigrada when these were seen feeding during microscopic examination and culture of the moss and liverwort samples.

Results

Identification of the algae

Forty species of algae were found at SIRS 2. Following the classification of Bourrelly (1966, 1968, 1970), they were identified as:

Cyanophyceae	*Aphanocapsa muscicola* (Menegh.) Wille; *Chroococcus pallidus** Naeg.; *Nostoc muscorum* Kuetz.; *Isocystis pallida** Woronichin; *Pseudanabaena catenata* Lauterb.; *Oscillatoria subtilissima* Vauch.; *Lyngbya perelegans* Lemm.
Xanthophyceae	*Chloridella* sp. A; *Monodus subterraneus* Boye Pet.; an unknown species of Pleurochloridaceae; *Gloeobotrys terrestris* Reisigl; *Botrydiopsis* sp.; *Gloeobotrys* sp.; *Heterotrichella gracillis* Reisigl; *Tribonema vulgare* Pascher; *Heterothrix* sp.
Diatomophyceae	*Eunotia fallax* A. Cleve; *Achnanthes lapponica* var. *ninckei** (Guerm. and Mang.) Reim.; *Pinnularia borealis** Ehr.; *Pinnularia mesolepta* var. *angusta* Cleve.
Euchlorophyceae	*Chlamydomonas chlorostellata* Flint and Ettl; *Chloromonas* sp.; two unknown species of Gloeocystaceae designated A and B; *Hypnomonas* sp.; *Chlorococcum humicolum* (Naeg.) Rabh.; *Rhopalocystis oleifera* Schussnig; *Chlorella homosphaera* Skuja; *Scotiella antarctica** Fritsch; two unknown species of Radiococcaceae designated A and C; *Myrmecia bisecta* Reisigl; *Chondrosphaera* sp.
Zygophyceae	*Cylindrocystis brebissonii* var. *minor* West and West.
Ulothricophyceae	*Stichococcus bacillaris* Naeg.; *Raphidonemopsis sessilis* Deason (var. ?); *Planophila* sp. A; *Microthamnion kuetzingianum* Naeg.; *Gongrosira terricola* Bristol; *Prasiola crispa** (Lightf.) Menegh. ("*Hormidium*" stage).

Illustrations and descriptions of these species will be given by Broady (in press). The algae marked with an asterisk (*) never developed in culture and were probably intolerant of the culture conditions. The remainder all grew in the media employed.

Vertical distribution of the algae

In deep cores. In both 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). Although both cores were taken in winter, it is thought that the distribution is also an indication of that of the previous summer. At the end of summer the site is solidly frozen which effectively fixes the algae in their summer positions and numbers.

TABLE I. VERTICAL DISTRIBUTION OF ALGAE IN SINGLE DEEP CORES

Date	*Percentage frequency at each depth**						*Total number of algae in core* ($\times 10^3$ cm.$^{-2}$)
	0–1·5 cm.	1·5–3·0 cm.	3·0–4·5 cm.	4·5–6·0 cm.	6·0–7·5 cm.	7·5–10·0 cm.	
July 1972	90	4	3	+	3	–	73
June 1973	79	9	7	2	2	1	174

* Data are from single cores at each sampling occasion.
\+ Less than 1 $\times$ 10^3 cm.$^{-2}$.
– Numbers not determined.

In the upper layers of the bryophytes. Counts were made on six types of algae (i–vi below). Other algae were observed in too low numbers for counts to be worthwhile (vii below). The micro-distribution of the total numbers of the six types is displayed in Fig. 1. Few algae were found below a depth of 6 mm. from the bryophyte-shoot apices.

i. Green and yellow-green unicells were frequently present either as single free-living unicells, micro-colonies of free-living unicells, or in small gelatinous colonies. It was usually impossible to recognize the different species as the cells were often filled with food-storage products and it was hard to discern the internal cell detail necessary for identification. *Botrydiopsis* sp., *Rhopalocystis oleifera* and *Chlamydomonas chlorostellata* were occasionally recognized. Rare cells of *Scotiella antarctica* and *Cylindrocystis brebissonii* var. *minor* were also seen. Numbers of cells in the micro-colonies were counted as accurately as possible.

These algae were mostly restricted to the upper 2·5 mm. of the plants, in the region of healthy green moss and liverwort tissue.

ii. Of the four members of the Diatomophyceae only *Eunotia fallax* was frequently seen, cells of the other three species being rare. *E. fallax* was present as single cells occasionally clustered in small micro-colonies but more often spread over the leaves and stems.

The cells reached maximum numbers at or slightly above the level where the healthy green tissue merged into the underlying yellow-brown tissue between 2·0 and 3·5 mm. below the shoot apices, very few being present at the apices of the plants.

iii. *Nostoc muscorum* occurred in two forms. First, as heterocystous trichomes much twisted and enclosed within an outer pellicle, the micro-thalli assuming various shapes from spherical, ellipsoidal and cylindrical to other more irregular shapes. Secondly, as straight heterocyst-free, often motile hormogones, sometimes with a conical terminal cell. The latter were formed by the fragmentation of the heterocystous thalli, followed by the rupture of the outer pellicle which allowed the release of the motile fragments. Both types were considered as equally ranking individuals for the purpose of the counts despite the considerable difference in size. Occasionally, the positions of dead and decaying *N. muscorum* thalli were noted.

The total count displayed in Fig. 1 indicates that *N. muscorum* has a similar dis-

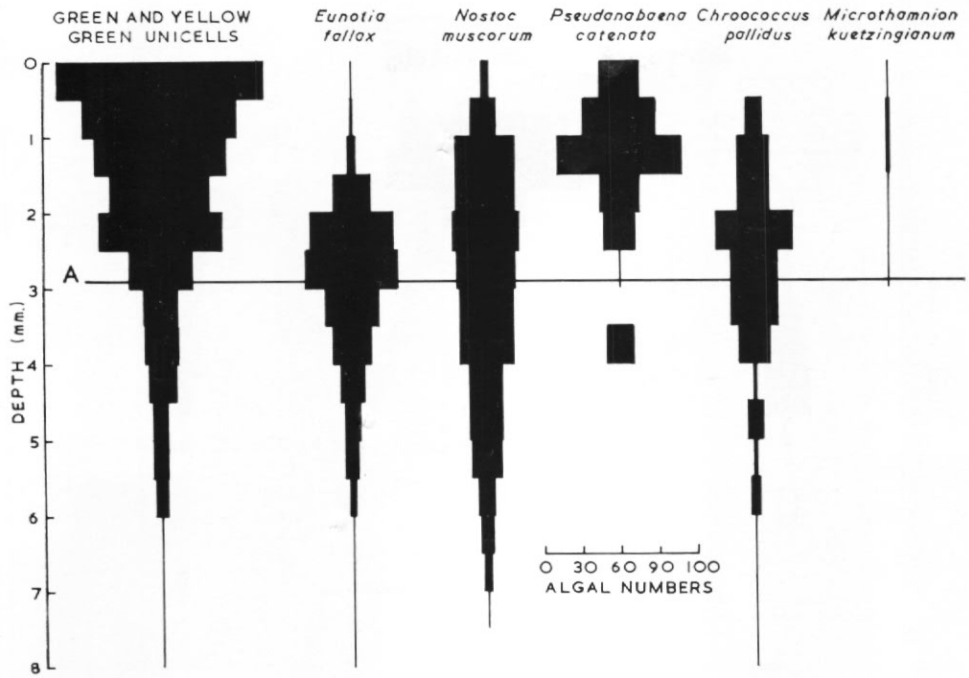

Fig. 1. The vertical micro-distribution of six types of algae. Total numbers of algae found on 88 bryophyte shoots. Line A represents the boundary between healthy green and the underlying yellowish brown bryophyte tissue.

tribution to *E. fallax*, with a few algae at the bryophyte-shoot apices, but the former occurs over a wider length of shoot with high numbers being recorded from 2 mm. above to 2 mm. below the region where the green and yellow-brown bryophyte tissue merged. Fig. 2 presents the numbers of this species in area B over a 3 month summer period. In January, all plants showed similar distribution patterns with an upper concentration of hormogones of *N. muscorum* between 0·5 and 2·0 mm. Many of these demonstrated a slow gliding motility. Below the healthy green tissue there was another concentration of *N. muscorum* in the heterocystous ensheathed form, mostly present between 3·5 and 5·0 mm. It was noted that these two concentrations occupied regions of the plant equal in depth to the positions of the shoot apex of the previous two summers (1972–73 and 1971–72). In the region of the shoot apex of the 1970–71 summer, a few dead colourless heterocystous thalli were recognizable. When plants from the same area were examined in February, no hormogones were present and most of the heterocystous algae were present between 1 and 2·5 mm., a position occupied in January by the hormogones. Dead thalli were present below 2·5 mm. The pattern was similar in March, and again no hormogones were present.

iv. *Pseudanabaena catenata* occurred as narrow filaments of varying length. Because of their fine structure, they fragment easily into short lengths and it is probable that many were overlooked, especially when they were present only in low numbers. However, each filament, irrespective of length, was regarded as an individual for the purpose of the count.

Most were present on the green healthy bryophyte tissue only, reaching a peak 1·5 mm. below the shoot apices. No significance is attached to the small concentration between 3·5 and 4·0 mm.

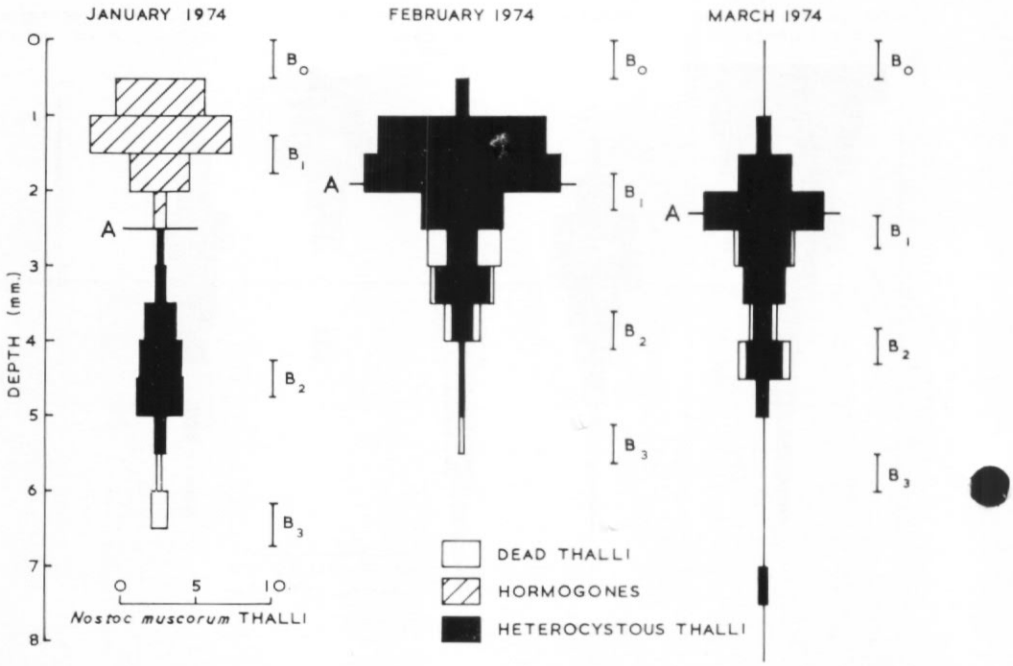

Fig. 2. The vertical micro-distribution of *Nostoc muscorum* along bryophyte shoots. The numbers of algae shown are the mean of six plants in January and of three plants in each of February and March. Line A represents the boundary between healthy green and the underlying yellow-brown bryophyte tissue, and the lines B_0–B_3 indicate the positions of the shoot apices of the current summer and at the end of successive previous summers.

v. *Chroococcus pallidus* was rarely seen in significant numbers. However, it was sometimes present in high numbers with a distribution similar to that of *E. fallax* with the gelatinous colonies thickly coating the stems and leaves.

vi. *Microthamnion kuetzingianum* was also infrequently observed and only in low numbers. The micro-thalli always consisted of from one to no more than ten cells. They were attached to bryophyte leaves and stems, fungal hyphae and organic detritus by the small terminal holdfast on the basal cell. Each thallus was regarded as a single individual for the purpose of the count.

vii. Other algae were seen in low numbers but were not counted. Gelatinous micro-colonies of *Aphanocapsa muscicola* containing up to *c.* 20 cells adhered to the plant surfaces. *Isocystis pallida* was rare and filaments of *Tribonema vulgare* and *Prasiola crispa* "*Hormidium*" stage were sometimes seen loosely lying on the plant surfaces.

Seasonal changes in algal numbers

Table II gives the mean counts in areas A, B and C for the period April 1972–April 1974. The three counting techniques were not equally efficient in estimating the numbers of each of the five categories in the table. Consequently, the data provided are the maximum values obtained for each particular type.

i. The data presented for the green and yellow-green unicells were obtained by the plate-culture count. The direct and m.p.n. counts were generally lower. *Scotiella antarctica*, *Prasiola crispa* and *Chondrosphaera* sp. did not grow in culture. The sole member of the Zygophyceae which was recorded in this site, *Cylindrocystis brebissonii* var. *minor*,

TABLE II. SEASONAL CHANGES IN NUMBERS OF ALGAE IN THE UPPER 1·5 cm. OF BRYOPHYTE CORES

Sampling date	*Numbers of algae with standard error** ($\times 10^3$ cm.$^{-2}$)				
	Green and yellow-green algae	Diatoms‡	*Nostoc muscorum*	*Pseudanabaena catenata*	*Chroococcus pallidus*‡
April 1972†	316 ± 65	66	75 ± 33	23 ± 15	0
July†	196 ± 59	2	42 ± 12	1 ± 0·5	0
August†	188 ± 44	–	24 ± 11	+	–
October†	84 ± 33	1	24 ± 12	+	0
November	816 ± 460	6	80 ± 30	5 ± 4	0
December	–	23	300 ± 150	117 ± 69	0
January 1973	108 ± 36	35	101 ± 60	41 ± 21	0
February	173 ± 80	19	47 ± 18	65 ± 48	0
March	205 ± 25	49	72 ± 35	85 ± 53	7
April†	489 ± 383	34	34 ± 23	2 ± 1	11
May†	204 ± 25	–	67 ± 35	40 ± 22	0
June†	101 ± 4	23	45 ± 31	1 ± 0·5	0
July†	146 ± 27	12	75 ± 67	4 ± 3	207
September†	67 ± 8	15	64 ± 15	1 ± 1	3
October†	119 ± 26	10	73 ± 16	1 ± 0·5	5
November†	335 ± 100	6	56 ± 54	38 ± 35	27
December	92 ± 11	13	232 ± 133	31 ± 24	0
January 1974	208 ± 135	41	358 ± 185	314 ± 269	4
February	203 ± 39	61	151 ± 76	138 ± 76	2
March	–	–	–	–	14
April†	–	–	–	–	87

* Data are means of three replicate cores at each sampling occasion.
† Winter counts.
‡ Data from bulked homogenates of the three replicate cores; no standard errors.
\+ Less than 1 $\times 10^3$ cm.$^{-2}$.
– No count made.

did not appear on the agar plates and only rarely in aqueous media. All four species were only rarely seen by direct observation and it is presumed that they occurred in low numbers in the site. It is considered that the majority of the green and yellow-green algae were detected by the plate count. Although the data in Table II indicate distinct peaks in numbers in November (when melt occurs) and again at the end of

the summer (April), the author places little reliance on this trend due to the inadequate sampling procedure and the highly aggregated distribution of these algae; this is emphasized by the very high standard errors for the November and April means. The situation is further complicated by the fact that the spring melt in 1972 commenced in early November but in 1973 it was a month later. The mean summer (November–March) count in 1972–73 was $325 \pm 150 \times 10^3$ compared with the 1972 winter (April–October) and 1973 winter (April–November) counts of $196 \pm 50 \times 10^3$ and $209 \pm 82 \times 10^3$ cm.$^{-2}$, respectively.

Only in the m.p.n. count were the algae identified on all occasions. The mean numbers of algae in summer and winter are shown in Table III. Only the five identified

TABLE III. NUMBERS OF GREEN AND YELLOW-GREEN ALGAE RECORDED IN SUMMER AND WINTER BY THE MOST PROBABLE NUMBER CULTURE-COUNT METHOD

Species	*Mean numbers of algae with standard error** ($\times 10^3$ cm.$^{-2}$)	
	Winter	*Summer*
Rhopalocystis oleifera	30 ± 6	46 ± 13
Radiococcaceae C	8 ± 7	7 ± 4
Microthamnion kuetzingianum	2 ± 1	6 ± 4
Chloridella sp. A	79 ± 33	72 ± 44
Monodus subterraneus	7 ± 2	12 ± 8
Others† (21 species)	10 ± 3	11 ± 1
TOTAL	136 ± 35	154 ± 50

* Data are means of all 11 sampling occasions in winter (April–October 1972 and April–November 1973) and eight sampling occasions in summer (November 1972–March 1973 and December 1973–February 1974).

† Individual counts of a single species on any one sampling occasion never exceeded 5×10^3 cm.$^{-2}$.

species occurred as more than 5×10^3 cm.$^{-2}$ on at least one sampling occasion. The remaining 21 species never exceeded this figure and were of minor importance. *Chloridella* sp. A and *Rhopalocystis oleifera* were dominant. No significant differences were apparent between the summer and winter means.

ii. The data for diatom numbers were obtained from the direct microscopic count. As the cores from areas A, B and C were bulked before counting, no standard errors could be calculated. Only *Eunotia fallax* was frequently seen and on each occasion constituted more than 95 per cent of the total count. *E. fallax* was intolerant of the growth media, rarely appearing in liquid media and never on agar. *Pinnularia mesolepta* var. *angusta* was occasionally seen in the m.p.n. cultures. In all the direct counts there were large numbers of empty diatom frustules, usually far outnumbering the cells with healthy contents. From five regular counts between February and July 1972, a mean of $28 \pm 6 \times 10^3$ living cells cm.$^{-2}$ and $329 \pm 56 \times 10^3$ empty frustules cm.$^{-2}$ were recorded.

In both summers there appeared to be a gradual increase in diatom numbers throughout the summer followed by a decline continuing until late winter. There was no apparent rapid increase corresponding with the spring thaw.

iii. *Nostoc muscorum* was recovered with greatest efficiency by the m.p.n. count in liquid medium. Although good growth was obtained on agar plates, the counts obtained by this method and by direct microscopic examination were generally lower. However, the latter method was advantageous in that the heterocystous thalli and hormogones could be distinguished. In culture both produced macroscopic colonies similar in appearance.

In both summers there was a large increase in numbers early in the season. In 1973 they decreased from the peak to a relatively constant level throughout late summer and the following winter, rising rapidly in December; this increase continued into January due to the late thaw in that year.

From November 1973 to April 1974 the direct count was used to provide information regarding the proportions of hormogones and heterocystous thalli comprising the total count (Table IV). When the site thawed in December, there was a large increase

TABLE IV. CHANGES IN NUMBERS AND LIFE STAGE OF *Nostoc muscorum* RECORDED BY DIRECT MICROSCOPIC COUNTS DURING A SUMMER

Sampling date	*Total number* of thalli* ($\times 10^3$ cm.$^{-2}$)	*Number of hormogones* ($\times 10^3$ cm.$^{-2}$)	*Number of heterocystous thalli* ($\times 10^3$ cm.$^{-2}$)
November 1973†	47	1	46
December	148	55	93
January 1974	216	75	141
February	217	37	180
March	186	17	169
April†	94	9	85

* Data are obtained from three bulked cores, one from each of areas A, B and C.
† Winter count.

in the number of hormogones from a low end-of-winter count in November. Maximum numbers occurred in January; they then declined until the end-of-summer number approached that of the previous November. In the 1972–73 summer it was also noted that many hormogones were present in December. These had not been seen in the previous winter counts nor were they seen in the following winter. Unfortunately, the two life stages were not distinguished in the direct counts over that period.

iv. *Pseudanabaena catenata* was detected most effectively by the m.p.n. count technique. Trichomes were rarely seen during direct microscopic observation of the core homogenates because of their pale colour and small size. The plate count produced consistently lower numbers than the m.p.n. count. This species apparently grows preferentially in a liquid medium.

A large increase in numbers occurred early in both summers and in the 1972 and 1973 winters only very low numbers were detected. The early winter count of $40 \pm 22 \times 10^3$ cm.$^{-2}$ in May 1973 was probably due to the sampling of a large aggregation of this alga and was not representative of the site as a whole.

v. *Chroococcus pallidus* was only occasionally seen in the direct count. It was intolerant of the culture conditions and never appeared in the plate or m.p.n. counts. The counts given in Table II are estimates of total cell numbers. The gelatinous colonies were not fragmented into single cells by homogenization, usually two or four cells remaining bound by a common mucilage.

The fluctuations in numbers are not thought to represent real changes with time but are due to the high aggregation of this species and the small number of cores removed. The mean monthly count of $18 \pm 11 \times 10^3$ cm.$^{-2}$ for the period April 1972–April 1974 is possibly a fair estimate of the typical standing crop over the site as a whole.

vi. Not included in the counts presented in Table II are four members of the Cyanophyceae, namely *Aphanocapsa muscicola*, *Isocystis pallida*, *Oscillatoria subtilissima* and *Lyngbya perelegans*. Small mucilaginous colonies of *A. muscicola* were occasionally recorded in the direct counts. Although capable of growth in culture it was never seen in the plate counts and in the m.p.n. counts only low numbers (less than $0{\cdot}2 \times 10^3$ cm.$^{-2}$) were observed even after the cultures were left to incubate for ten weeks. *I. pallida* never appeared in culture and was rare in direct microscopic observation. *O. subtilissima* and *L. perelegans* never appeared on the culture plates and only occasionally in m.p.n. cultures in numbers less than 1×10^3 cm.$^{-2}$. Both were rare in direct microscopic observation. It is considered that all four of these species are numerically unimportant members of the algal flora.

Horizontal distribution of the algae

Considerable variation was found in the horizontal distribution of several algae.

i. The results of the plate counts on areas A, B, C and D are given in Table V. Neither diatoms nor *C. pallidus* were detected using this technique and *P. catenata* did not grow well on agar plates. However, despite these limitations, the counts revealed differences in the algal floras of the four areas.

The total counts for areas A, C and D were similar, while that for area B was rather higher. *M. subterraneus* was dominant in the drier area (D) but it was poorly represented in the other areas where *N. muscorum*, *R. oleifera* and, in area A only, *G. terrestris* were most frequent. Since *M. subterraneus* was also dominant in the *Polytrichum alpestre–Chorisodontium aciphyllum* turf of SIRS 1 (Broady, 1977), this species clearly has a preference for drier moss communities.

ii. Differences were apparent between the algal floras of the two liverwort (*Cephaloziella varians*) areas E and F (Table VI). The green and yellow-green algae often could not be identified because of the limitations of the direct microscopic counting technique. However, their total counts in the two areas were similar, although there were large differences in the counts of *E. fallax*, *N. muscorum* and *C. pallidus*. In area F the latter two species were dominant whilst in area E, *E. fallax* and green and yellow-green unicellular algae were the major forms.

iii. Macroscopic green gelatinous forms had a restricted distribution. Numerous rocks and stones protruded through the moss carpet but in places the moss grew over them, forming slightly raised drier moss mounds. The gelatinous colonies frequently occurred around the edges of the stones and on the summits of the small hummocks. They were irregularly shaped and up to 5 cm. in width. Such colonies were never found amongst the larger, wetter continuous stands of bryophytes but only in these drier niches. Microscopic examination revealed that they were almost entirely composed of *Chondrosphaera* sp. This alga would not grow on BBM agar plates or in aqueous media but other algae growing epiphytically on the gelatinous colonies did develop. These were all typical of the moss epiphytic algal flora (see above).

Other aspects of algal ecology

Interactions of the algae with other members of the micro-flora. Loose associations between algal cells and fungi and bacteria were seen on numerous occasions. During microscopic

TABLE V. MID-SUMMER COMPOSITION OF THE ALGAL FLORA OF FOUR MOSS-DOMINATED AREAS OF THE SITE RECORDED BY A PLATE-CULTURE COUNT

Area	*Percentage of total count with standard error**												*Total count with standard error** ($\times 10^3$ cm.$^{-2}$)
	Nostoc muscorum	*Pseudanabaena catenata*	*Chlamydomonas chlorostellata*	*Chloromonas* sp.	Gloeocystaceae B	*Rhopalocystis oleifera*	*Monodus subterraneus*	*Gloeobotrys terrestris*	*Gloeobotrys* sp.	*Chloridella* sp. A	*Botrydiopsis* sp.	Other algae	
A	10±6	0	+	0	5±2	37±5	4±1	23±3	3±1	2±1	1±0·5	15±2	325±29
B	62±14	3±2	5±3	0	1±1	6±3	2±1	1±0·5	4±3	8±3	1±0·5	7±1	553±163
C	33±23	6±2	5±3	0	8±5	30±10	9±4	+	+	1±1	+	7±2	352±203
D	0	3±2	3±1	4±1	11±1	1±1	54±8	0	5±1	+	13±5	6±1	285±108

Areas A, B and C were almost pure *Calliergon sarmentosum*; in area D *C. sarmentosum* and *Chorisodontium aciphyllum* were co-dominant.
* Data are the means of four cores (A, B and C) and six cores (D).
+ Less than 1 per cent ($<1 \times 10^3$ cm.$^{-2}$).

TABLE VI. MID-SUMMER COMPOSITION OF THE ALGAL FLORA OF LIVERWORT-DOMINATED AREAS RECORDED BY DIRECT MICROSCOPIC COUNTS

Area	*Percentage of total count*					*Total count** ($\times 10^3$ cm.$^{-2}$)
	Eunotia fallax	Other diatoms	Green and yellow-green unicells	*Nostoc muscorum*	*Chroococcus pallidus*	
E	46	3	50	1	0	271
F	1	+	23	36	39	961

* Data are obtained from six bulked cores from each area.
+ Less than 1 per cent (<1 $\times 10^3$ cm.$^{-2}$).

examination of the gelatinous colonies hyaline and melanized fungal hyphae and bacteria were seen coating the surface and sometimes penetrating the mucilage. Algal cells, developing on microscope slides buried in the upper layers of the bryophytes, were usually surrounded by a halo of bacteria, even when the cells appeared quite healthy. Both gelatinous and non-gelatinous algae were coated in this manner. Wefts of fungal hyphae frequently grew amongst micro-colonies of algal cells, particularly green and yellow-green unicells. This was often observed during the direct microscopic examination of moss and liverwort shoots in the analysis of the vertical micro-distribution of algae. The algae usually appeared healthy and no fungal penetration of their cells was seen. Similar growths were occasionally present around *N. muscorum* thalli. Lower down some moss plants there were large numbers of bacteria around the dead thalli of *N. muscorum*. The small branching thalli of *M. kuetzingianum* were sometimes observed attached to fungal hyphae and *P. catenata* was seen lying along lengths of hyphae.

Algae as a food source for soil invertebrates. The collembolan *Cryptopygus antarcticus* was found to have complete and fragmented algal cells in its gut contents and direct microscopic examination of these showed several species to be present. Apparently healthy cells of *R. sessilis*, *E. fallax*, *C. brebissonii* var. *minor*, *P. catenata*, *C. pallidus*, *A. muscicola*, *M. kuetzingianum* and *M. subterraneus* were infrequently identified. Of more common occurrence were unidentifiable free-living green unicells and small gelatinous groups of green cells. The gut contents also contained empty cell walls and ruptured cells with their contents spilling out while dead *N. muscorum* thalli, H-shaped cell-wall fragments of *T. vulgare* filaments and complete empty frustules and fragments of *E. fallax* were all occasionally present. Despite the many types of algae seen in the guts, 56 of which were examined, only five had algae or their remains as the dominant content, fungal hyphae usually being more abundant. Dead, empty moss and liverwort leaf cells and unidentifiable, amorphous, fine-grained material were also often dominant. Similar algae were seen in the direct microscopic examination of faecal pellets, some cells having retained their healthy appearance despite passage through the gut. Twenty guts were dissected from animals and placed on BBM agar plates. Ten developed algae, over 100 being produced from one gut. Five faecal pellets, out of a total of 52 plated on BBM, also produced algal growth, which, though having only a low frequency of recovery, demonstrates that some algae will survive passage through the gut.

Information on the other groups of soil invertebrates was restricted to occasional observations. Ciliate Protozoa and rhizopodal amoebae were seen containing green and yellow-green unicellular algae and short lengths of *P. catenata* during examination of the m.p.n. culture tubes. The ciliates were seen only in the lowest dilution tubes, suggesting that their numbers in the bryophytes was low. Small flagellates were frequently seen in the higher dilutions but none contained algae. *Vorticella striata* (Smith, 1973), seen in culture and during direct microscopic observation of the bryophyte shoots, also never contained algae.

Only one rotifer, *Habrotrocha* sp., was seen browsing on green unicellular algae.

Tardigrades were observed infrequently on the bryophyte shoots. On two occasions circumstantial evidence suggested that the individuals were feeding on algae. The animals had greenish gut contents despite being present on yellow-brown decaying moss and liverwort. The only green material present was of algal origin. Also, the tardigrades were seen in the bryophyte leaf axils where most algae were lodged.

Discussion

The presence of most algae in a restricted region 0–6 mm. down the bryophyte shoots (Fig. 1) is probably correlated with the lack of light penetration into the moss carpet, where a dense interwoven matrix of shoots forms a more or less closed canopy. In the turf-forming SIRS 1 mosses the tall, erect parallel shoots allowed sufficient light penetration for most algae to occur down to 8–14 mm. (Broady, 1977).

Apical growth of the bryophytes produces new tissue, which has to be colonized by the algae if they are to maintain their presence in the site (see Broady, 1977).

The green and yellow-green unicells consist of species with and without motile stages in their life cycles. Those with motile stages are able to distribute themselves via the water film over the surface of the vegetation. Those without have to depend on external agencies for their distribution into the upper layers similar to *M. subterraneus* in SIRS 1. This is a chance process with only occasional cells being re-distributed. It might be expected that these two types of algae would have different distribution patterns, the former being able to reach the plant apices in this wet site and the latter showing maximum numbers lower down the plants, as in SIRS 1. Most cells were present at the plant apices (Fig. 1). These were possibly cells of the zoospore-producing *R. oleifera*, one of the dominant algae in the site (Tables III and V). In the drier area (D) *M. subterraneus* was dominant (Table V), while the motile forms such as *R. oleifera* were not successful probably because of the lack of water films. Although distinct early and late-season peaks were reached, these are considered to be a reflection of inadequate sampling of aggregated populations. More intensive investigations are required of algal vertical distribution in relation to water availability and to the relative proportions of motile and non-motile algae.

E. fallax had a similar distribution to that postulated for the non-motile green and yellow-green unicells. Although possessing small terminal raphes, structures associated with motility in diatoms, no movement was seen in this species and it probably depends on its chance re-location up the bryophyte shoots.

Nostoc muscorum possesses a life cycle with a motile stage which enables it to maintain a population in the higher lighter regions. The information in Fig. 2 and Table IV provides evidence for the growth model presented in Fig. 3. In early summer the *N. muscorum* thalli are present as twisted heterocystous trichomes within an outer pellicle. These are aggregated around the positions of the previous year's shoot apices *c.* 3 mm. below the current year's apices (A). Soon after the site thaws, the trichomes fragment at the heterocyst positions and motile hormogones are released. These move up the plants at the same time as bryophyte growth commences (B). Later in summer the hormogones reach the position of the old terminal bud from where the current year's growth commenced and here a concentration of

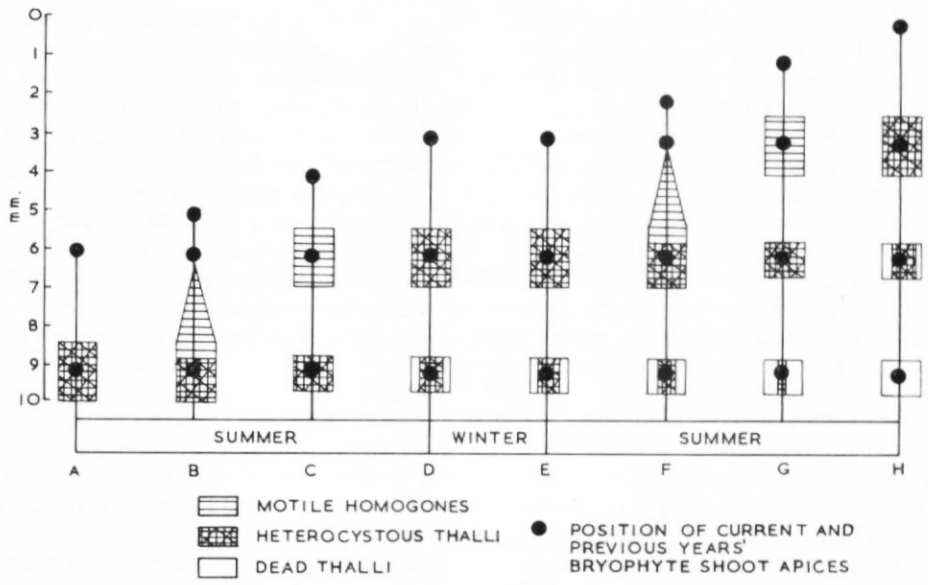

Fig. 3. The growth of *Nostoc muscorum*, a postulated mechanism by which the alga keeps pace with moss growth.

N. muscorum thalli occurs. Lower down the plant a residual population of heterocystous thalli remains which did not release hormogones. Further growth of the plants places this lower concentration in the shade and the thalli become moribund. The upper hormogones form heterocystous thalli similar to those present at the beginning of summer (D). It is in the heterocystous form that most of the *N. muscorum* overwinter (D and E). As from the spring melt at the start of the following summer, the process is repeated. Individuals remaining low down the bryophyte shoots die due to further shading (F, G and H).

Lazaroff and Vishniac (1961) found that *N. muscorum* in culture produced motile hormogones after light activation of the heterocystous stage. In the present study the fragmentation is possibly a result of a stimulus on development of the higher summer light levels after snow has melted from the site.

Motility of the trichomes of *P. catenata* allows it to maintain a summer population mostly within the top 2 mm. of the bryophyte apices.

Slow movement has been reported in some unicellular blue-green algae (Lund, 1950). However, none was observed in *C. pallidus* and the micro-distribution of the cells was typical of that postulated for non-motile cells such as *M. subterraneus* in SIRS 1 (Broady, 1977).

The summer increases in the numbers of *N. muscorum* (Table II) occur when the overwintering heterocystous stage fragments. Each thallus releases several hormogones which each form a single colony in culture, resulting in the increased counts. The higher counts are not an indication of algal production, but of the formation of more "propagules". Most production probably occurs later in summer when the hormogones produce a pellicle and become the long convoluted heterocystous trichomes. During this period, numbers of *N. muscorum* detected in the culture count decrease (Table II; January–March 1973).

There are no such complications in the summer increase in numbers of *P. catenata*, in which fragmentation of the trichomes during the summer growth period rapidly produces a high population. However, this alga is intolerant of the winter conditions when the population falls to a low level.

E. fallax demonstrated a summer increase in numbers. If the re-distribution of the cells

on to the new upper bryophyte surfaces, followed by their reproduction, balanced the death rate caused mainly by shading, then the population numbers should remain constant throughout the summer period of bryophyte growth as postulated for non-motile algae in SIRS 1 (Broady, 1977). However, numbers increased in both summers (Table II) and reproduction of cells re-located higher up the plants more than compensated for the losses. Over the winter months there was a gradual decrease in numbers and, like *P. catenata*, this alga is apparently intolerant of the winter conditions.

The latter two species build up a high summer population, thereby ensuring the survival of some individuals for renewed growth the following summer.

The considerable variations in the horizontal distribution of the algae, both qualitative and quantitative, do not necessarily correlate with changes in the bryophyte cover. Pure *Cephaloziella* (areas E and F) had different algal floras (Table VI). Here a difference in water status may have affected the algal flora without affecting the composition of the macroscopic vegetation which has a wider ecological amplitude. Low redox levels have been shown to benefit the growth of blue-green algae (Fogg and others, 1973). The high water content of SIRS 2, which, in many parts if permanently saturated by glacial melt water, may be responsible for such conditions in some parts of the site. In such areas, numbers of *N. muscorum* and *C. pallidus* may be high, as in area F, which was wet and boggy.

In the superficially similar *Calliergon*-dominated areas A, B and C there were also significant differences in the algal floras (Table V) which may also be related to differences in the water status. Area D, towards the drier edge of the site, was partly composed of invading turves of *Chorisodontium aciphyllum* and had a flora intermediate between that of the relatively dry SIRS 1 (Broady, 1977) and the wetter areas A, B and C of SIRS 2. Although *M. subterraneus* was dominant in both area D and SIRS 1, the numbers were considerably lower in the former, *c.* 150×10^3 cm.$^{-2}$ compared with *c.* $1{,}000 \times 10^3$ cm.$^{-2}$ in *Chorisodontium* on SIRS 1. Area D was possibly too wet for rich growth of *M. subterraneus* but too dry for the more typical SIRS 2 algae found in the wetter areas A, B and C.

The macroscopic mucilaginous colonies of *Chondrosphaera* sp. occurred in drier habitats around the edges of stones and on small raised hummocks. However, they did not occur amongst the continuous carpets of drier moss towards the edge of the site. In such situations, the colonies were possibly unable to establish growths amongst the tightly packed bryophyte shoots despite the presence of more favourable drier conditions.

Variation in the growth rate of the bryophytes may be important in determining the algal flora. It was postulated that in SIRS 1 variations in the growth rate of *Polytrichum* affected the numbers of algae inhabiting different areas (Broady, 1977). In SIRS 2, rapid bryophyte growth in more favourable areas may cause a reduction in the standing crops of those algae least able to keep pace, particularly those without a motile stage. This mechanism may be more prevalent than in SIRS 1 because of the often higher growth rates of carpet-forming mosses, up to 4 cm. yr.$^{-1}$, compared with up to *c.* 1 cm. yr.$^{-1}$ in the turf-forming mosses (Collins, 1976).

Local variations in the nutrient status may also be of importance. Scattered bird droppings may inhibit or stimulate the growths of different algae depending on their concentration and state of decomposition. Through some areas of the site there may be a higher water flow bringing in nutrients and oxygenated water, whereas other areas may be largely stagnant and low in nutrients and redox levels. Further work is required to study the influence of these environmental factors on the horizontal distribution of the algae. Similarly, since bryophyte composition varies according to the water regime of the habitat and this largely determines their growth form (Gimingham and Smith, 1971), further investigation of the algal composition of the principal mosses in various communities should also reveal interesting differences in their horizontal distribution.

As in SIRS 1, the algae are producers of organic material which is assimilated by both

the heterotrophic micro-flora and the soil invertebrates. The decomposition of dead cells and the release of organic products from living cells is probably of importance in stimulating the growth of bacteria and fungi, and possibly of the bryophytes in which they occur. Few dead remains of algae were recognized even when bryophyte shoots were heavily coated with living algae, suggesting that decomposition of these must be rapid. Only the silica frustules of diatoms were common and it appears that, due to the rather inert property of silica, the re-cycling of these is a slow process.

The browsing of algae by soil invertebrates is not thought to be important in restricting algal numbers. Collembola, probably the major consumers, had algae only as a minor constituent of their guts. Few invertebrates were observed feeding during microscopic examination of bryophyte shoots, despite the high numbers of algae often present.

From the present knowledge, it is impossible to estimate the amount of algal material produced annually. The production of green and yellow-green algae is particularly difficult to gauge as the aggregated populations masked possible changes in numbers. *P. catenata*, despite its high summer population, is unimportant because of the small size of its filaments. For *N. muscorum*, the high counts, large size and the observed growth of the trichomes in late summer probably combine to make it the most important algal producer in the site. This is unusual in such an acid site (*c.* pH 5·0; Tilbrook, 1973), although the pH of the micro-habitat occupied by the *Nostoc* may be higher than this value. Jurgensen and Davey (1968) found no growth of *Nostoc* below pH 5·0 in North America. Fogg and Stewart (1968) and Horne (1972), on Signy Island, found that *Nostoc commune*, either free-living or in the lichen *Leptogium puberulum* (quoted as *Collema pulposum* (personal communication from R. I. L. Smith)) occurred on only neutral or alkaline substrata and was absent from acid areas. They did not examine an area such as the present site. Whether *N. muscorum* makes a significant contribution to the nitrogen status by the fixation of atmospheric nitrogen requires further study.

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