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The spatial distribution of microalgae on Antarctic fellfield soils

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Abstract: The horizontal and vertical distributions of cyanobacteria and algae on soil polygons on Signy Island were investigated. Soil chlorophyll concentrations increased from the centre to the edge of the polygons. Similar distributions of the non-motile genera, such as *Pseudanabaena* and *Nostoc*, were observed, whereas the motile taxa, *Phormidium* and *Pinnularia*, were evenly distributed across the polygon. *Phormidium autumnale* was the most widespread taxon, and other Oscillatoriaceae were also important, although large differences in community composition between polygons were observed. Most of the algal biomass was concentrated near the surface of the soil, although chlorophyll degradation products were found to depths of up to 8 cm. Examination of the soil profile by fluorescence microscopy indicated that a large proportion of the microflora occurred in the zone 0–1 mm below the surface, and scanning electron microscopy confirmed that few algae occurred on the soil surface. It is suggested that this may be a desiccation-avoidance strategy. Vertical migration of the motile microalgae to the soil surface was not observed in the field, but could be induced in the laboratory in the presence of excess water, although no diel cycle to this movement was observed.

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Introduction

Fellfield ecosystems are common in both the Arctic and Antarctic (Aleksandrova 1980); those of the Antarctic are characterized by an almost entirely cryptogamic flora, largely of mosses and lichens (Smith 1972, 1988, 1990a, Kappen 1985). However, even the most mature Antarctic fellfields include areas of visually barren soil fines (Chambers 1966a, 1967), and similar areas of soil fines also occur in the phanerogamic fellfields of the northern tundra (Chernov 1985, Aleksandrova 1988). In both regions frost-heave and particle sorting produce patterned ground, typically polygons, circles and stripes (Washburn 1979). Fellfield soils are subject to extremes of environmental stress, principally freezing (Chambers 1966b, Walton 1982) and desiccation (Northover & Grimshaw 1967), in addition to the physical disruption of an unstable environment in which organisms may be mixed below the soil surface (Chambers 1967).

Cyanobacteria and eukaryotic algae, hereafter referred to jointly as microalgae, are primary colonizers of fellfield soils and constitute a large proportion of the soil flora (Broady 1986, 1989, Smith & Coupar 1987, Wynn-Williams 1985, 1986). Once established the microbial flora increases the stability of the soil by particle aggregation and hence promotes the establishment of the moss flora (Wynn-Williams 1990a). A similar process may also take place in the mature fellfields following disruption of the established flora. The margins of polygons have been shown to contain greater numbers of plant propagules than the centres of polygons (Smith & Coupar 1987, Smith 1987), and a similar distribution of biologically derived organic compounds has also been observed (Tearle 1987). It is possible that the microalgal colonizers may also be found in greatest numbers around the edges of polygons.

Previous studies on the soil cyanobacteria and algae have been restricted to observations of the soil surface (Wynn-Williams 1985, 1986, Davey 1991) and no information is available on the vertical distribution of these organisms.

This paper describes the horizontal and vertical distribution of cyanobacteria and microalgae in the soil polygons on an immature fellfield.

Materials and methods

Study site and sampling methods

The investigation was carried out on the British Antarctic Survey Fellfield Ecology Research Programme (FERP) site at Jane Col on Signy Island, South Orkney Islands; an immature fellfield, 150 m a.s.l., which has only recently been exposed by the retreating ice-cap (British Antarctic Survey 1982, Smith 1985, 1990b). This site consists of sorted stone polygons (0.5–2 m x 0.2–1 m) with a centre of soil fines (mean particle size 45 μm — Wynn-Williams 1986) surrounded by larger stones (Chambers 1967). Two polygons were selected for detailed study, the first having no visible vegetation and the second supporting small patches of the

moss *Ceratodon* at the boundary between the fines and larger stones.

All samples were collected in January or February when algal populations were close to their seasonal maximum (Davey 1988a, 1991). Those samples used for SEM studies were collected during early morning when the soil was still frozen, and those for the rest of the investigation around midday when the soil was easily cored.

During February 1988 three 30 mm diameter cores were taken to a depth of *c.*100 mm from the centre of each polygon. On return to the laboratory these were sectioned and selected layers (0–5, 5–10, 20–25, 40–45 and 80–85 mm) sub-cored to give 16 cores of 12 mm diameter from each polygon. In addition, 16 cores of 12 mm diameter were also taken to a depth of 5 mm at distances of 8, 16, 24, 32, 40 and 50 cm from the centre of each polygon. The cores at 50 cm were outside the polygons themselves, but were taken in small patches of soil fines (<20 mm diameter). Cores of larger particles (*c.* 5 mm diameter) were also collected from outside the polygons.

The investigation was placed in a wider perspective by the collection of four cores (two centre, two edge) from a further 21 soil polygons at Jane Col, and examination of the soil flora by light and epifluorescence microscopy of the soil surface as described below.

Chlorophyll analysis

Four cores from each set were used for chlorophyll *a* analysis using the method (4.4.1) of Marker *et al.* (1980). Cores were frozen overnight to maximise extraction efficiency (Hansson 1988) and pigments extracted using 90% methanol. Absorbance was measured at 665 and 750 nm before (A_{b665} and A_{b750}) and after (A_{a665} and A_{a750}) acidification to 10^{-3} M HCl for 1 h. Total chlorophyll *a* concentration (Chl), and the degraded (P) and undegraded (C) fractions were then calculated using equations derived from those of Talling *et al.* (1978) and Marker *et al.* (1980) respectively :-

$$[Chl]\ (mg\ m^{-2}) = 139.(A_{b665} - A_{b750}).v / d.a$$

$$[C]\ (mg\ m^{-2}) = 316.((A_{b665} - A_{b750})-(A_{a665} - A_{a750})).v / d.a$$

$$[P]\ (mg\ m^{-2}) = [Chl] - [C]$$

where, v = volume of solvent (ml), d = spectrophotometer path length (cm) and a = area of core (cm^2).

Light microscopy

Four cores from each polygon were used for microscopic examination of the flora. The cores were placed in Petri dishes, wetted with distilled water if necessary, a coverslip placed on the surface, and incubated at 5°C at an irradiance of 40 µmol m^{-2} s^{-1}. After 24 h the coverslip was removed, along with the attached algae (Broady 1979), and examined microscopically using brightfield and epifluorescent illumination. Twelve photomicrographs of the algal flora from each site were taken at 100x magnification, and the negatives were returned to the UK for analysis of the composition of the algal flora using a Seescan Image Analyser (Seescan Ltd., Cambridge). This method quantifies the algal populations in terms of proportions of coverage of the examined area and is described in detail in Wynn-Williams (1988). The surface of the core was also examined by epifluorescence microscopy to reveal any algae that did not attach to the coverslip. These accounted for only a small proportion of the algal community (usually <1%), but were measured and added to the total algal coverage as determined by image analysis.

Eight cores were incubated at a temperature of 10°C and a photon flux density of 50 µmol m^{-2} s^{-1} for 14 days (conditions adequate for any potential growth to occur (Davey 1988a)), four being supplemented with the culture medium described by Davey (1988b) and four with distilled water. At the end of the incubation period these cores were examined and the flora analysed microscopically as described above.

Ten further cores (12 mm diameter, 5 mm deep) were collected from each site and frozen to -20°C. These were then scored on the underside, fractured and the rim of the core trimmed flat whilst still frozen. The core was then placed on a microscope slide, fracture-face uppermost, and the vertical distribution of algae within the top 5 mm of the soil determined using epifluorescence microscopy, counts being made in bands 100 µm deep.

Scanning electron microscopy

Blocks of soil measuring 10x10x1 cm were collected from a number of polygons on the Jane Col site without disturbing the soil surface. These were stored at -20°C in square Petri dishes and returned to the UK for scanning electron microscopy. Small sub-samples (5x3x2 mm) were excised from the soil, whilst still frozen, and placed on pieces of coverslip. The temperature was reduced to -210°C using slushed nitrogen and the samples freeze-dried. A small amount of 0.5% methyl cellulose (Sigma Chemical Co. M 7140) was introduced from near the bottom of the sample to bind the material, but was not allowed to reach the sample surface. Samples were then sputtered with gold and the soil surface examined using a Jeol CX100 Temscan electron microscope in scanning mode.

Vertical migration of microalgae

The possibility of migration of the motile components of the microalgal community to the surface was investigated in three experiments during January and February 1990. In each of the first two experiments (13–14 and 24–25 January) 100 coverslips were placed on the surface of each of three polygons and left overnight. Over the following 24 h four coverslips were removed every hour, placed on a microscope slide with a drop of Lugol's iodine solution as preservative

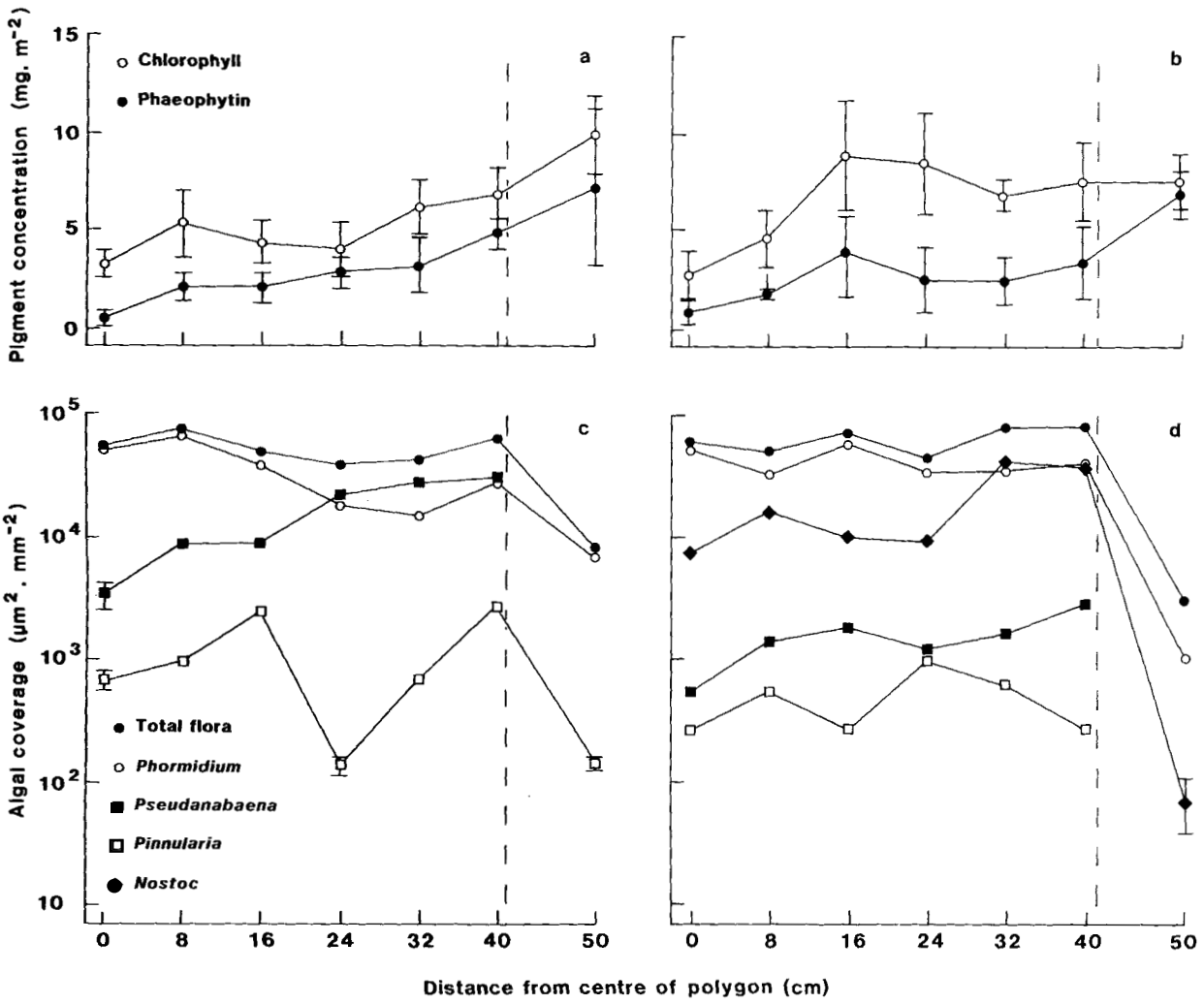

Fig. 1. The horizontal distribution of plant pigments (**a** & **b**) and microalgae within the upper 5 mm of soil polygons (**c** & **d**). Polygon lacking macrovegetation (**a** & **c**), polygon surrounded by mosses (**b** & **d**). Dashed line indicates position of the edge of the polygon. Error bars indicate standard errors.

and sealed with nail varnish. The numbers of *Pinnularia* cells and lengths of *Phormidium* filaments were determined at a later date. In the third experiment (14–15 February) 100 14 mm diameter cores were collected from each of four polygons and returned to the laboratory. Coverslips were placed on the surface of each core, two sets with the addition of a few drops of distilled water and two sets without. All cores were maintained at 5°C in a constant temperature room on a 18:6 light:dark cycle, the light period consisting of 6 h at 40, 6 h at 400 and a further 6 h at 40 µmol m^{-2} s^{-1}, the lower irradiance being supplied by fluorescent tubes and the higher by a high intensity lamp. Following 24 h acclimatization four coverslips were removed from each set every hour and treated as above.

Results

Horizontal distribution of the microalgae

The distributions of the dominant taxa of algae and cyanobacteria and the soil chlorophyll concentration across the two polygons investigated are shown in Fig. 1. A total of 10 species from as many genera were observed. Both polygons were dominated by the cyanobacteria *Phormidium autumnale* (Agardh) Gomont and *Pseudanabaena catenata* Lauterborn, with the diatom *Pinnularia borealis* var. *rectangularis* Carlson as sub-dominant. In addition, the polygon with some macro-vegetation around the edges supported a large population of *Nostoc* sp. The other taxa observed were *Achnanthes lapponica* var. *ninckei* (Guermeur et Manguin) Reimer, *Chlamydomonas chlorostellata* Flint et Ettl, *Planktosphaerella terrestris* Reisigl, *Cylindrocystis brebissonii* var. *minor* West et West, *Cosmarium undulatum*

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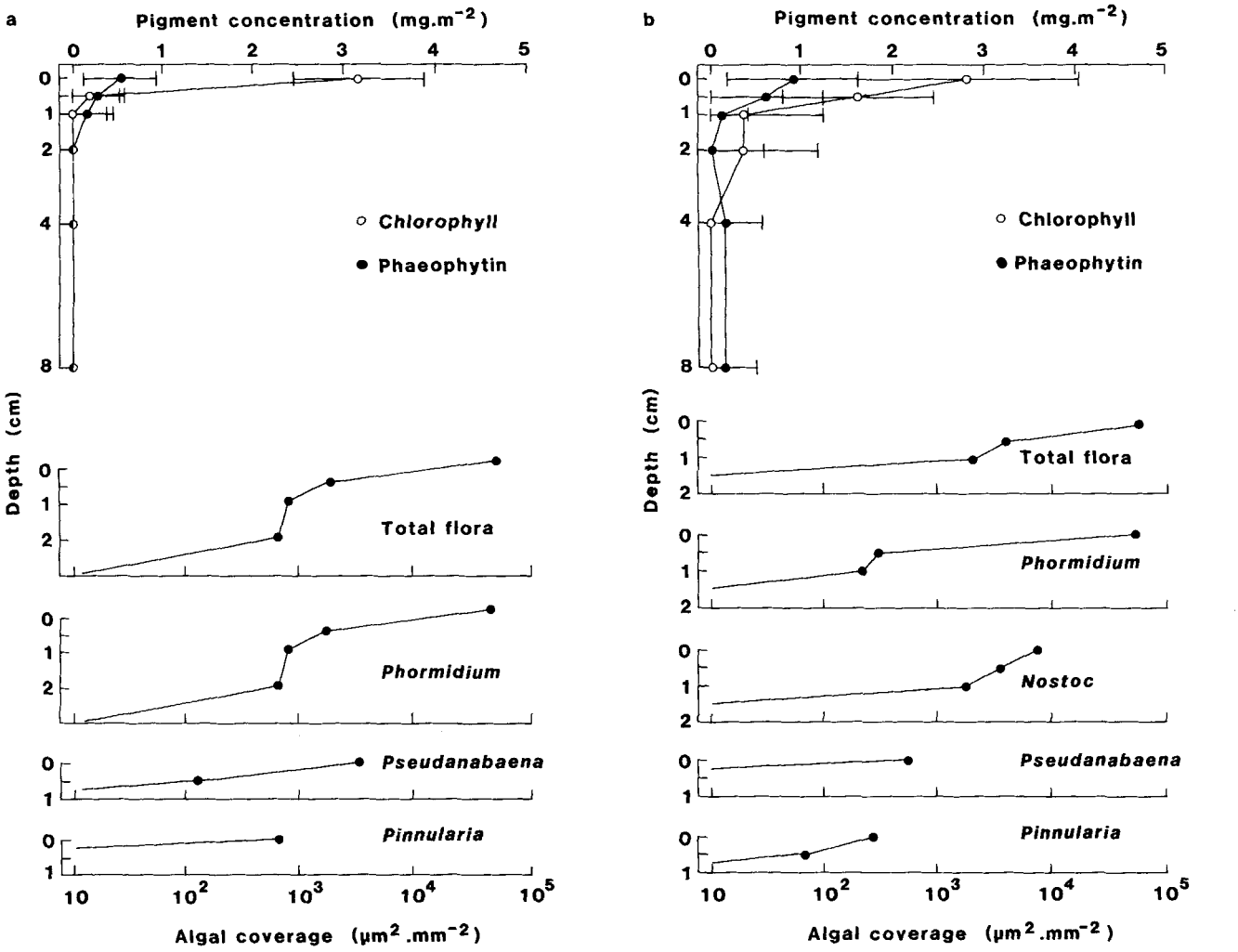

Fig. 2. The vertical distribution of plant pigments and microalgae at the centre of soil polygons. **a.** polygon lacking macrovegetation, **b.** polygon surrounded by mosses. Error bars indicate standard errors.

var. *minutum* Wittrock and *Netrium* sp., although in insufficient amounts for any pattern in their distribution to be observed.

The total algal cover did not alter across the polygons, although the concentration of chlorophyll *a* and its degradation product, phaeophytin, significantly increased from the centre to the edge of the polygon ($P = 0.01$ for chlorophyll, $P = 0.05$ for phaeophytin).

There were major differences between the distributions of individual taxa. The motile taxa, *Phormidium* and *Pinnularia*, showed no consistent trend in cover across the polygons, although cover of *Phormidium* declined somewhat towards the edge of the polygon without macro-vegetation. In contrast, coverage of the non-motile taxa, *Pseudanabaena* and *Nostoc*, increased towards the edges of the polygons. The areas of fines outside the polygons all had high pigment concentrations but low numbers of algae.

The less detailed analysis of algal and cyanobacterial distribution from 21 further polygons on Jane Col demonstrated the importance of the Oscillatoriaceae. *Phormidium autumnale* accounted for 78% (range = 0-99%) of the microalgae observed and other Oscillatoriaceae a further 11% (range = 0–80%). The one polygon in which no Oscillatoriaceae were observed was covered with mosses and lichens.

Incubation of the samples in the presence of either additional water or growth medium led to little change in the soil flora. Coverage of most taxa declined during the period of incubation, although that of *Nostoc* increased in samples in which it occurred. No additional taxa were revealed by the incubation process.

Vertical distribution of the microalgae

The vertical distributions of algae and cyanobacteria in the soil at the centre of the polygons are shown in Fig. 2. In both

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cases the microflora was concentrated in the upper layer of the soil. In general, the cyanobacteria were found to slightly greater depths than the diatom *Pinnularia*. The two polygons differ in the distribution of chlorophyll within the soil column. At the site without macro-vegetation chlorophyll *a* was confined to the surface and 0.5 cm layers, although phaeophytin was found slightly deeper. At the site with macro-vegetation around the edge chlorophyll *a* was found to a depth of 2 cm and phaeophytin to 8 cm. This difference was possibly due to chlorophyll release from the surrounding vegetation. Incubation of the samples in the presence of either additional water or growth medium promoted some growth in samples from 2 cm deep in which no algae had been recorded in the initial observations, possibly an indication of the survival of propagules to these depths. No growth was observed in deeper samples.

The distributions of microalgae in the top 5 mm of the soil are shown in Fig. 3. These again show differences between the motile and non-motile taxa. *Nostoc* was concentrated in the top 500 μm (median = 0.15 mm, mean = 0.24 mm, sd = 0.36 mm, $n = 1163$) with much of the population at or near the surface, and only small aggregations of filaments at greater depths. In contrast, *Phormidium* (median = 1.11 mm, mean = 1.51 mm, sd = 1.27 mm, $n = 1000$) and *Pinnularia* (median = 0.72 mm, mean = 1.15 mm, sd = 1.12 mm, $n = 449$), although concentrated in greatest numbers near the surface, were spread over the entire 5 mm depth examined.

Examination of the soil surface by scanning electron microscopy confirmed these results. Far fewer algae and cyanobacteria were observed on the surface than would be expected from the examination of coverslip samples, which concentrated the microflora at the surface. However, both cyanobacteria (Fig. 4a) and *Pinnularia* (Fig. 4b) were observed at the surface in numbers to be expected from the observations of fracture faces by fluorescence microscopy.

Investigation of possible migration of the microalgae to the soil surface indicated largely negative results. Virtually no cyanobacteria or diatoms were collected at the soil surface in either of the field experiments or in the laboratory experiment in which no additional water was added to the soil. In contrast, in the laboratory experiment in which water was added to the samples both diatoms and cyanobacteria were collected at the soil surface in numbers similar to those obtained from other samples using the coverslip technique. However, there were no significant diel differences in the numbers of microalgae collected.

Discussion

This investigation has shown that *Phormidium autumnale* is the most widespread and dominant species of microalga occurring on the fellfield soils of Jane Col, Signy Island. This observation agrees with that of Greene *et al.* (1967) who described the Antarctic distribution of *P. autumnale* as circumpolar, and added that there were more records of *Phormidium* than any other genus of cyanobacterium. Studies on the physiology of *Phormidium* have shown that it can grow well under typical fellfield conditions and that it is able to survive desiccation, and to a lesser extent freezing (Davey 1988*a*, 1989), often aided by the production of polyols (Tearle 1987). *Phormidium* also produces large amounts of mucilage (Castenholz 1982) that can bind soil particles, often resulting in mats of cyanobacterial filaments surrounding unicellular algae and inorganic material (Davey 1989).

The intra-polygonal distributions of the motile taxa varied from those of the non-motile taxa. Non-motile algae and cyanobacteria were found concentrated towards the edges of the polygons, as would be predicted from the movements of

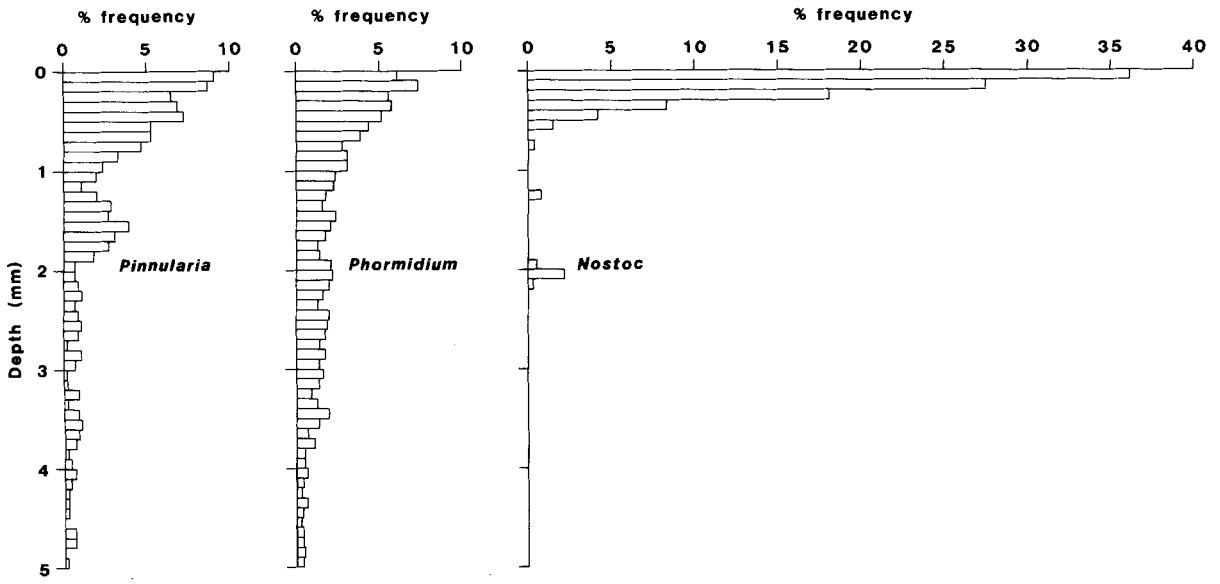

Fig. 3. The vertical distribution of microalgae in the top 5 mm of soil from the centre of polygons.

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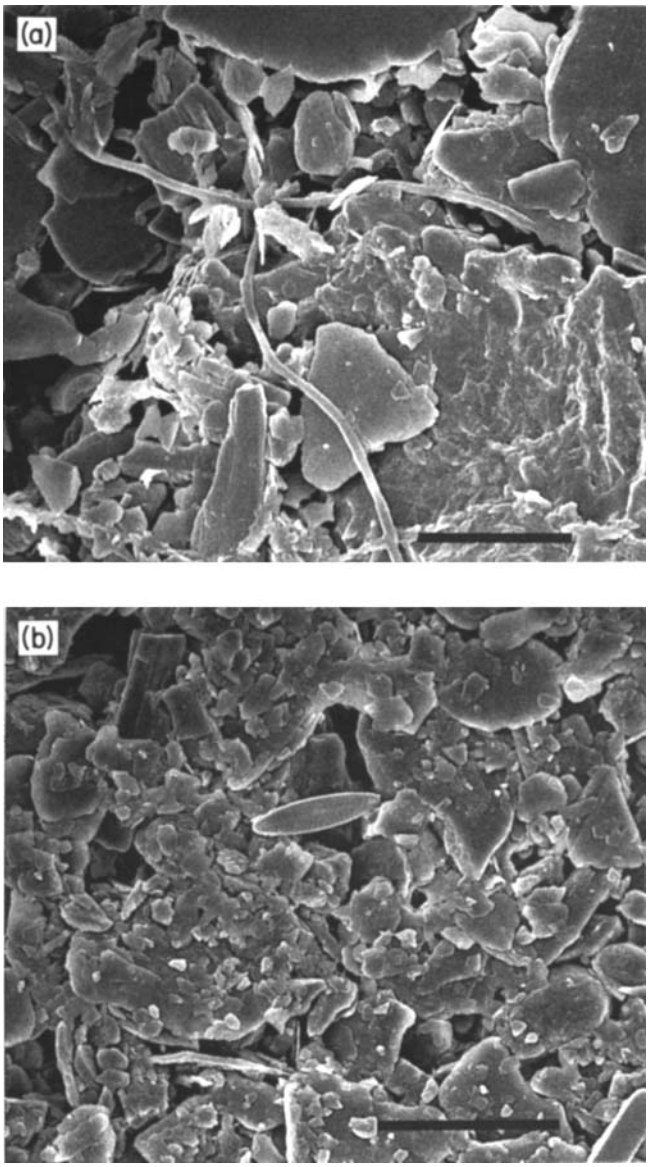

Fig. 4. Scanning electron micrographs of microalgae from fellfield soil polygons. **a.** Filaments of *Phormidium autumnale* partially on the soil surface, **b.** Cell of *Pinnularia borealis* var. *rectangularis* on the soil surface. Scale bars = 40 μm.

soil particles within the polygon and distribution of plant propagules (Chambers 1967, Smith 1987). However, the motile species were found to be evenly spread across the polygon, suggesting that there was some active divergence of individuals. Motility provides a mechanism whereby these organisms can counteract the unstable nature of the substratum (Chambers 1966a). The production of mucilage during movement promotes the formation of soil aggregates (Bailey *et al.* 1973), and hence enhances the soil stabilization process.

The horizontal distribution of plant pigments is less easy to interpret. The increase in concentration of chlorophyll towards the edge of the polygon may have been due to the influence of the surrounding vegetation or the presence of moss propagules in the soil, although none of the latter were observed by epifluorescence microscopy. Such a possibility is supported by the lack of any increase in total algal flora across the polygon and the presence of high concentrations of chlorophyll outside the polygon in areas of low algal biomass.

It is notable that *Nostoc* occurred on only one of the polygons investigated, where it accounted for a large proportion of the population. It was not found in the other polygon studied in detail, nor in any of the samples from other polygons on Jane Col. However, in previous studies it has been observed, in foliose form, in several areas of Signy Island (Fogg & Stewart 1968, Horne 1972, Broady 1979) and was recognized by Smith (1972) as forming one of two algal sub-formations on the island, primarily in areas where there is an increase in base status of the soil. In all cases where *Nostoc* has been found it has accounted for a large proportion of the community. It is clear from these observations that *Nostoc* is able to survive and grow on fellfield soils, and in fact possesses advantages over some other taxa, being able to fix nitrogen in a nutrient-poor environment (Davey 1986), and having a thick mucilagenous sheath (Broady 1979). It is curious that it does not occur on a larger number of polygons or dominate the ecosystem to a greater extent. It is possible that differences in the physio-chemical nature of the polygons in which *Nostoc* occurred promoted its establishment and/or growth. Further observations are required on both inter-polygon variation and the process of colonization of the soils.

The vertical profiles demonstrate that the microalgae are concentrated in the upper few millimetres of the soil, but, in most cases, are not actually at the soil surface. The *Nostoc* population, being non-motile may be regarded as a marker for the distribution that occurs as a product of growth of the microalgae and mixing of the soil. This suggests that growth is occurring in the near-surface layers, with little mixing to depths below 500 μm. The greater occurrence of motile populations deeper in the soil indicates either active movement of the motile component of the flora through the soil or a greater turnover of the soil in these polygons.

In addition, the SEM studies have confirmed that most individuals do not occur at the soil surface. The two main advantages experienced by organisms living just below the surface are the avoidance of the high irradiance and water stress. Positive phototaxis in *Phormidium autumnale* has been described from 5–10000 lux (*c.* 0.1–200 μmol m^{-2} s^{-1}) and maximal at 2000 lux (*c.* 40 μmol m^{-2} s^{-1}) (Nultsch 1961). The observations reported here indicate that the microalgae do not migrate to the soil surface at any time of day unless free water is available, when the populations concentrate on the soil surface even at high irradiances. Therefore, it may be concluded that desiccation-avoidance is the primary reason for the algal distribution. This conclusion is supported by the observations of cyanobacterial populations on the soil surface in transparent cloches where humidity is increased (Wynn-

Williams in press) and of growth of microalgae of the same genera on stone surfaces in nearby streams (Hawes 1990).

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