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MICROBIAL COLONIZATION PROCESSES IN ANTARCTIC FELLFIELD SOILS—AN EXPERIMENTAL OVERVIEW

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Abstract: The process of colonization of Antarctic fellfield soils by microorganisms has two phases: Firstly, the immigration, survival and establishment of microbial propagules themselves, and secondly the stabilization of the soil for subsequent colonization and establishment by mosses, lichens and invertebrates. Dominant amongst primary microbial colonizers are the phototrophic cyanobacteria and algae. Not only do they introduce organic nutrients into the microhabitat but they also have a structural function. Filaments of several dimensions frequently form a mesh over the surface of the soil. This mesh often has a canopy structure of fine filaments closely admixed with the mineral soil grains, overlain by a layer of broader, longer filaments. This structure may provide a rich grazing zone for micro-invertebrates such as protozoa and nematodes. Microbial filaments, clusters and unicells frequently have mucilaginous sheaths or capsules which may cement mineral grains together and improve soil crust stability. The combination of filaments and mucigel promotes the formation of microbial "rafts" which are dispersed by wind or water. The diverse microbiota of these compound propagules is likely to improve their chances of successful colonization of unpopulated soil surfaces. Phototrophic microbes can be distinguished in mixed natural communities of undisturbed soil crusts by selective filtration of their autofluorescence spectra. Heterotrophs can be distinguished after staining. The population can be selectively quantified by television image analysis (TVIA) using criteria of pigmentation, size and morphology.

1. Introduction

Of the approximately 2% of ice-free land in Antarctica, the majority of it is mineral fellfield having either no visible vegetation or only a discontinuous cover of cryptogams. The structure of maritime Antarctic fellfields at locations such as Signy Island (Fig. 1) is heterogeneous, and is governed by annual disruption by freeze-thaw cycles with concomitant frost heave (CHAMBERS, 1967). This process "sorts" the mineral components into gradients of size classes ranging from very small silt particles in the center of frost polygons (Fig. 2), through small stones round their periphery, to surrounding boulder fields. This natural sorting of fine particles in the center of frost polygons provides an eminently suitable flat substratum for the direct examination of colonization processes with minimal disruption of the microhabitat.

In areas where moisture (the prime regulator for life in Antarctic fellfields) is available for at least part of the year, there is colonization by microorganisms which may initiate the development of more diverse communities. The function of the microbes is

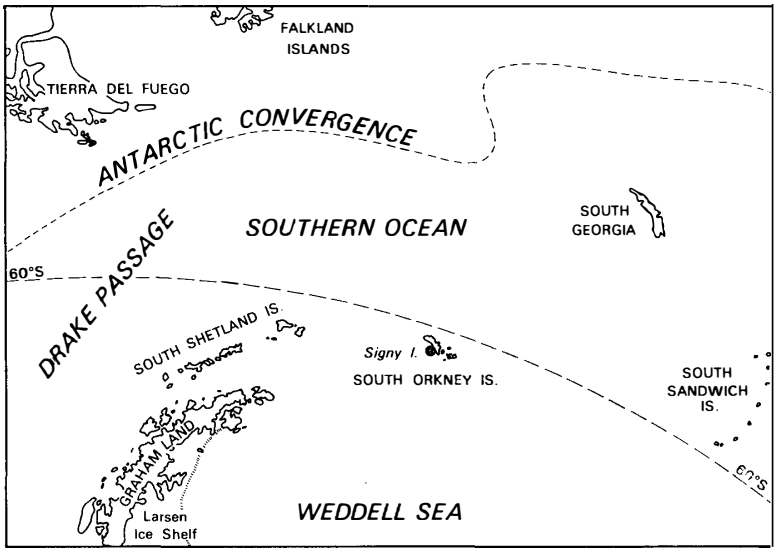

Fig. 1. Map of the Southern Ocean showing Signy Island in relation to other land masses.

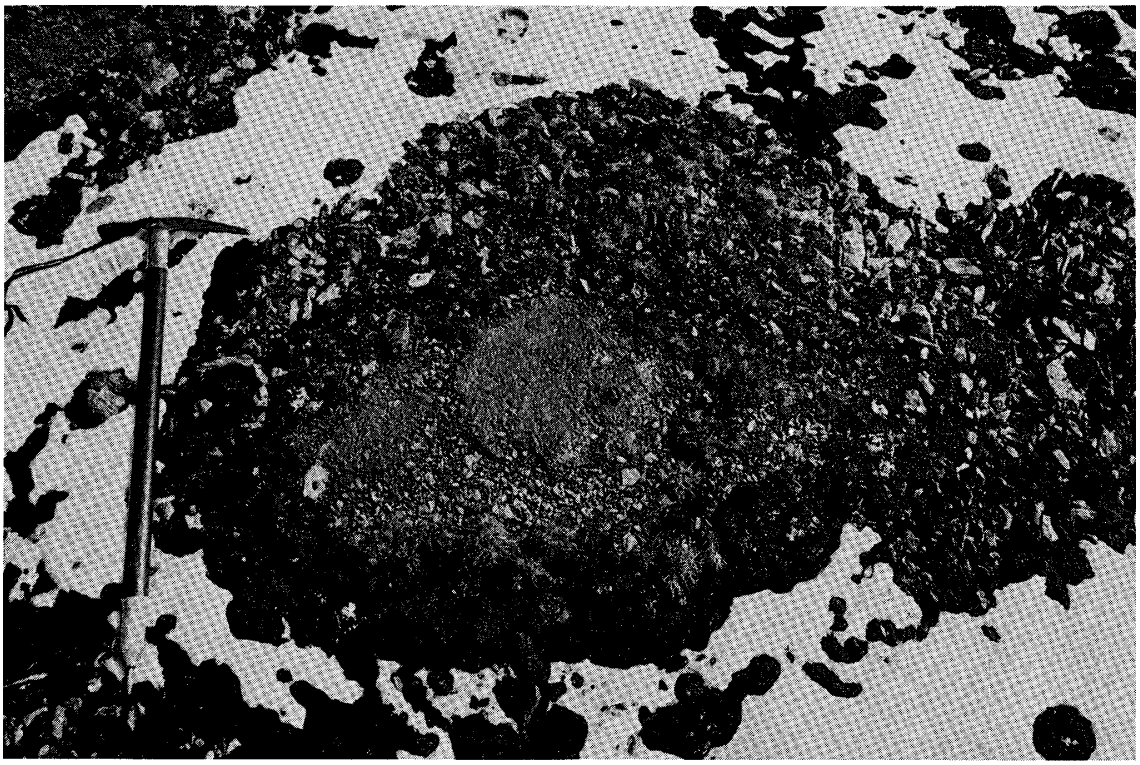

Fig. 2. Sorted frost polygon in fellfield soil at Signy Island, showing the central portion of fine mineral particulate material used for microbial colonization studies.

basically threefold: firstly, the physical stabilization of a substratum which is disrupted by a variety of physico-chemical stresses, predominantly freeze-thaw and wet-dry cycles; secondly, the supply of organic nutrients including potential 'compatible solutes'. These are solutes which can be accumulated to high intracellular concentrations, without

inhibition of enzymes or membrane function, to compensate for osmotic stresses due to external solute concentration during freezing and desiccation; thirdly, the re-cycling of organic and inorganic nutrients within the fellfield ecosystem. The process of colonization and stabilization of the mineral substratum requires microbial colonizers with diverse abilities, summarized by WYNN-WILLIAMS (1986), and is believed to follow a developmental sequence of uncertain duration (Fig. 3).

The dominant microbes in such primary communities are cyanobacteria and algae which, as phototrophs, are the initial primary producers which drive the ecosystem

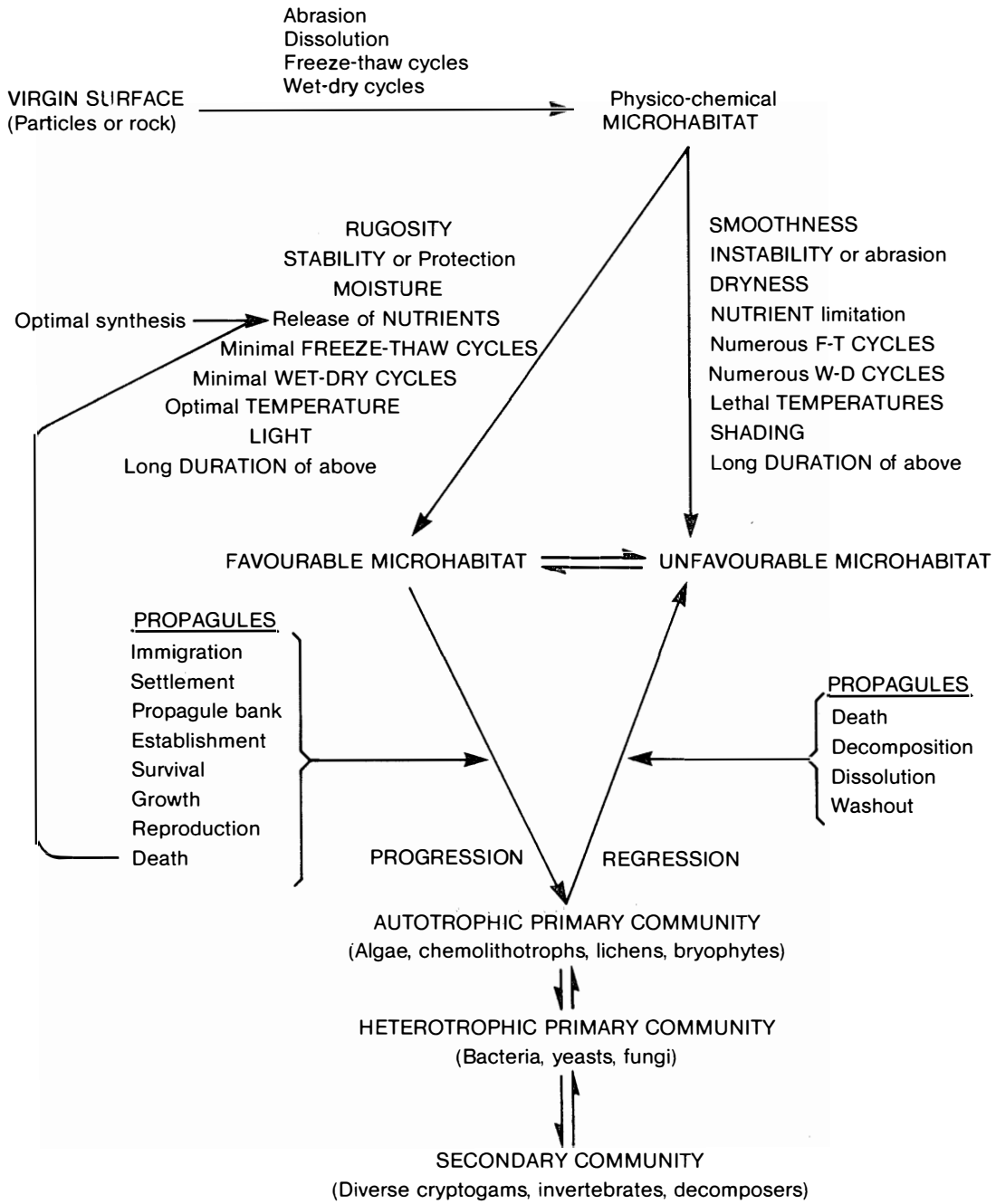

Fig 3. Potential sequence of colonization processes in maritime Antarctic fellfield soils.

(WYNN-WILLIAMS, 1989a). Associated with them are heterotrophic bacteria, and to a lesser extent yeasts and other microfungi. Microbial grazers include protozoa (SMITH and TEARLE, 1985) which show metabolic adaptations to the fellfield environment (HUGHES and SMITH, 1989). There is subsequent or concomitant colonization by mosses and liverworts (SMITH, 1985). The low species diversity amongst microbial colonizers in the Antarctic makes the fellfield ecosystem eminently suitable for studying colonization processes.

Cyanobacterial and algal filaments frequently form "rafts" which enmesh other microbial cells in a mucilaginous matrix (WYNN-WILLIAMS, 1985). They also form a mesh over the surface of the soil, providing structural stability whilst cementing the soil particles together to form a crust suitable for community development (NEDWELL and GRAY, 1987).

Since most biological activity occurs in the top few millimeters, the soil is best observed from above. Epifluorescence microscopy combined with television image analysis (EFTVIA) can be used to quantify the dimensions of microorganisms (FRY, 1988) and extent of their colonization of the substratum (WYNN-WILLIAMS, 1989a). The autofluorescence of phototroph pigments permits observation without staining (SCHREIBER, 1980), limiting the disruption of the community to merely mounting the excised crust in a photofading retardant (WYNN-WILLIAMS, 1985). This apparently non-invasive technique can be further refined by visual identification of different groups of phototrophs, not only by their morphology but also by selective blocking of their fluorescence emission using barrier filters (WYNN-WILLIAMS, 1989a). Heterotrophic microbes such as bacteria and fungi can be stained with fluorochromes such as Acridine Orange before mounting (TROLLDENIER, 1973).

The relative simplicity of the frost polygon habitat permits the quantification of the effects of physical and chemical perturbations. The mineral soils are often nutrient deficient, and the availability of water, inorganic nutrients and energy substrates is transient. Moreover, the growing season is short, and the ground temperatures are usually low but are very variable, ranging at Signy Island from $-25°C$ in winter to over 30°C. The studies reviewed here include (a) the effect of inorganic and organic amendments on the microflora, (b) the effect of improving ambient field conditions by using plastic cloches, and (c) the potential influence of substratum particle size in the process of microbial settlement process from meltwater.

2. Materials and Methods

2.1. Study site

The British Antarctic Survey Fellfield Ecology Research Programme (FERP) site at Jane Col, Signy Island, South Orkney Islands (60°43'S, 45°35'W) is a fellfield area at 150m a.s.l. It has been fairly recently exposed by ice retreat and has frost-sorted polygons with a very limited moss and lichen vegetation. Microbiological studies on sorted polygons were conducted on the central quartz-mica schist fines of mean grain size 45 μm (range 13–132 μm). The mean water-holding capacity (WHC) of the fines was $>75\%$, and they were saturated (100% WHC) for much of the spring when meltwater was abundant. The mean ($\pm$s.d.) annual precipitation for the period 1974–1987

($n=11$) measured near sea level at the research station (2.2 km distant from the Jane Col site) was 270.5 ± 48.7 mm. For the period of experimentation 1985–1987 ($n=3$) it was 317.3 ± 72.9 mm. The flat topography of the Jane Col site ensures that the soil is wet for most of the growing season. A meltwater runnel contained either standing or flowing water at every visit throughout the summers of 1984–1985 and 1987–1988 (D. D. WYNN-WILLIAMS, unpubl.)

2.2. *Enrichment studies*

Full details are given in WYNN-WILLIAMS (1986). Petri dishes (9 cm diameter) were filled with minimally-disrupted soil crust slices and replaced in the resulting hole in the polygon fines. They were then enriched with sterile nutrient solutions as summarized in Table 1. After 10 days, *ca.* 3 mm thick crusts were sliced off sample cores 15 mm diameter × 15 mm deep, placed on microscope slides, and mounted in Citifluor AF2 photofading retardant (Citifluor Ltd., City University, London, U.K.) (WYNN-WILLIAMS, 1985).

The crusts were examined at magnifications of ×100 and ×400 using a Leitz Laborlux microscope fitted with a Ploemopak epifluorescence illuminator with a 50W HBO200 mercury arc lamp and a Leitz I2 filter block. This had a BP450–490 nm excitation filter, an RKP510 nm dichroic mirror, and an LP515 nm suppression filter. The red (chlorophyll and phycocyanin) and gold (phycoerythrin) fluorescing cells and trichomes of algae and cyanobacteria were photographed using an Olympus OM2 microscope on automatic setting. Kodak Technical Pan film 2415 rated at ISO 125 was used to produce monochrome negatives, and Fujichrome 400 (ISO 400) was used for color slides. To quantify heterotrophic microorganisms, the soil crusts were partly air-dried in the dark at 4°C and re-moistened to near-saturation with a 67 mg l^{-1} dilution of Acridine Orange (AO). They were drained before mounting in Citifluor AF2 for photography (WYNN-WILLIAMS, 1985).

Initially, an AMS Ltd. (London Rd., Pampisford, Cambridge, U.K.) System III

Table 1. Experimental amendments added to fellfield fines at Jane Col, Signy Island, relative to locally available nutrients.

Nutrient	Jane Col content[a]	Amendments (final concentration)
Water	*ca.* 75% WHC	80% WHC (Control)
Na	6	Not added
K	7	In 0.2% (v/v) in Bolds Basal Medium without nitrate[b] (minerals)
Ca	12	
Mg	4	
PO_4-P	4	0.015% (w/v) K_2HPO_4 (P)
NO_3-N	0.01	In 0.010% (w/v) NH_4NO_3 (N)
NH_4-N	0.01	
Organic C	1000 (total)	1.0% (w/v) glucose (Glucose)
		50% (w/v) moss homogenate (Moss)
		Undiluted snow algae homogenate (Algal)
		0.01% guano extract (Guano)

[a] mg per 100 g^{-1} dry weight of soil.

[b] NICHOLS and BOLD (1965).

image analyzer was used to quantify the images on the resulting 35-mm negatives and slides. Data were processed by an Apple microcomputer to give outputs of cell/trichome count (C), area (A), percentage area fraction ($\%A$) and intercept (I, proportional to total length). From these data, the following dimensions were derived using formulae recommended by AMS Ltd.:

Total propagule length,	$L_T=\pi\times I/2$
Individual propagule length,	$L=\pi\times I/2C$
Propagule diameter,	$D=2A/\pi I$
Total propagule biovolume,	$V_T=A^2/2I$.

These data were analyzed for Minimum Significant Difference (MSD) between treatments (Tukey-Kramer method).

2.3. Settlement studies

The particle size-range of the natural substratum was simulated using three grades of carborundum cloth immersed in a meltwater runnel at Jane Col in January 1985. Simplifying the grain morphology to cubic form, their side lengths were *ca.* 5 μm, *ca.* 75 μm and *ca.* 265 μm, respectively. Sheets 50-mm square were secured to stones in the runnel for 10 days. They were then recovered and photomicrographed for TVIA, before and after staining with AO, mounted in immersion oil after gently rinsing in a 1 : 10 dilution of Citifluor AF2 (WYNN-WILLIAMS, 1985). The data were analyzed for Minimum Significant Difference by the Tukey-Kramer method of Multiple Comparison Analysis (SOKAL and ROHLF, 1981).

2.4. Studies of the heterogeneity of colonization

Cores 15 mm $\times$ *ca.* 10 mm deep were taken at 5 cm intervals on a 25 cm $\times$ 25 cm grid in the center of a frost polygon in the Jane Col site. They were transported to the BAS research station at $<$15°C and held at 4°C, usually for $<$3 h, before treatment. The upper 3 mm of the soil crust was excised and transferred with minimal disruption to a microscope slide for direct examination mounted in Citifluor AF2. Observations were made with a Leitz Laborlux 12 microscope and a Ploemopak epifluorescence illuminator fitted with a 50-W HBO-200 mercury arc lamp. A Leitz N2.1 green excitation filter block (band pass excitation at 515–560 nm, beam splitting by dichroic mirror at 580 nm, and long pass barrier filter at 580 nm) was used to quantify the autofluorescing cyanobacteria and algae using a $\times$10 objective resulting in a magnification equivalent to $\times$100.

The microflora was quantified using a Panasonic WV1850 extended-red Newvicon camera coupled to a Seescan I3000 Image Analyzer (Seescan Ltd., Cambridge, U.K.). The system comprised a Solitaire Plus processing system with 256 $\times$ 256 $\times$ 8 bit resolution, combined with a high resolution monitor displaying monochrome images with pseudocolor superimposed. Of the wide range of processing available, the optimal combination for the present samples was a high pass filter and contrast enhancement to aid thresholding of the object relative to the background on a 0–128 grey-scale. Exclusion conditions based on area and elongation were used to select for specific cell

morphologies and to eliminate electronic "noise" and debris.

The length (L), breadth (B), elongation (E) and biovolume (V) of component cells and their total area (A) of coverage were determined from the perimeter (P), area and intercept (I) of the images of the microorganisms. The use of P and A for deriving dimensions obviates much of the error due to cell orientation relative to the pixel array. The derivation of cell length and breadth assumes a rod or filament to be a cylinder with hemispherical ends:

$$\text{Area of a rod,} \qquad A_{\text{rod}}=(L-B)B+\pi(B/2)^2$$

$$\text{Perimeter of a rod,} \qquad P_{\text{rod}}=2(L-B)+\pi B$$

Solving for B and L using $x=[-b\pm\sqrt{(b^2-4ac)}\,]/2a$
where $a=\pi/2$, $b=-P$, and $c=2A$

$$B=[P-\sqrt{(P^2-4\pi A)}\,]/\pi$$

$$L=(P/2)+B(1-\pi/2).$$

These equations were optimal for short rods and good for cocci and long filaments, whether straight, curved or spiral. All measurements were checked against both computer-generated standard cell images (FRY, 1988) and against cell measured using a calibrated eyepiece graticule.

Biovolume was calculated from the formula:

$$V=(\pi B^2/4)(L-B/3).$$

2.5. Cloche studies

To investigate the effect of elevating the ambient field temperature and moisture regimes on the soil crust microflora, a small plastic cloche was established in December 1984 near the north side of the Jane Col site. It was made of plastic transparent to visible light and measured $570\times290\times150$ mm high. The cloche was secured over part of the central fines of polygon containing a little visible moss near its periphery. Small vents in the top were left open to permit gentle air circulation. Snow accumulation was not greatly different inside relative to an adjacent unenclosed control plot of the same visual appearance and surface area.

Initially and after 3 years (18 summer months permitting growth), five replicate cores (15 mm diameter $\times$ *ca.* 10 mm deep) were taken at random from the mineral fines in the cloche and adjacent control. They were transported to the BAS field station at <15°C, and held at 4°C in the dark pending examination. The surface crusts were treated as for the heterogeneity experiment.

During the summer of 1988, duplicate zeolite-containing plastic Ambrose spheres (WALTON, 1982) were used to obtain integrated temperature data by measurement of their temperature-dependent water-uptake for six *ca.* 10-day periods. Soil moisture content was determined gravimetrically and expressed as % water-holding capacity (WHC).

3. Results

3.1. Enrichment studies

The results in Table 2 show an apparent stimulation of phototrophs primarily by glucose as an energy/carbon source and secondarily by inorganic nitrogen. However, the most consistently influential stimulant for the total heterotrophic microflora was moss extract, although guano extract, inorganic N and minerals were also beneficial.

Table 2. Effect of amendments on colonizer dimensions on fellfield polygon soil at Jane Col.

Microbial propagule dimension	Extent or absence of stimulation of microbial colonizers by amendments. Analysis of MSD[a] between treatments
Algae and cyanobacteria	
Total area	Glucose>Control, Minerals and Guano
Total count	Glucose>Control, Algal and Guano
	Nitrogen>Control
Total length	Glucose>Control and Guano
Total heterotrophs	
Total area	Moss>Control, Glucose, Algal and Guano
	Minerals, N and P>Control
Total count	Moss>Control, Glucose, Algal and P
	Guano>Control and Glucose
	Minerals>Control and Glucose
	N, Minerals, P, Algal and Glucose>Control
Total length	Moss>Control, Glucose, Algal, N, P, Guano and Minerals
	Minerals>Control and Glucose
	Guano>Control and Glucose
	P and N>Control

[a] Minimum Significant Difference ($P<0.05$) between treatments, computed by Multiple Comparison Analysis relative to controls and each other. Sequence indicates decreasing order of magnitude of the dimension.
>significant difference.

3.2. Settlement studies

The distinctive and varied morphology of the cyanobacteria dominating the fines raised the possibility of an interaction of certain morphotypes with mineral grains of different sizes. Filamentous forms are on occasion seen to be tangled around grains, and small unicells can aggregate in the interstices between grains. However, there was no general consistency in the significant differences for colonization parameters between distinct grain sizes (Table 3). This is highlighted when significant difference in a particular parameter (such as total biovolume and mean colonizer cell diameter) is detected between substrata of similar grain size (fine replicates 1 and 2). Consistency is, however,

Table 3. Effect of substratum grain size on the retention of algal and cyanobacterial propagules in a meltwater runnel at Jane Col fellfield site during 10 days of immersion.

Microbial	Significant difference (MSD[a]) between grade of carborundum as affecting retention of propagules
Total area	Fine 1[b] and Coarse > Fine 2 and Medium
Total count	Coarse > Fine 2
Total length	Medium > Fine 2, Coarse and Fine 1
Total biovolume	Fine 1 > Fine 2, Coarse and Medium Medium > Fine 2 and Coarse
Mean length	Medium > Coarse and pooled Fine Fine > Coarse
Mean diameter	Fine 1 > Fine 2, Coarse and Medium Medium > Fine 2 and Coarse
Mean biovolume	Coarse, Fine 2 and Medium > Fine 1

[a] Minimum Significant Difference ($P<0.05$) between treatments, computed by Multiple Comparison Analysis relative to controls and each other. Sequence indicates decreasing order of magnitude of the dimension.
> significant difference.

[b] Two sets of fine grade cloth were included and treated separately as a spatial control.

apparent for an interaction between trichome length and medium grain size (75 μm mean side length) which was colonized by significantly longer filaments than either coarser or finer substrata. It is evident from these data that factors other than mere size and morphotype are also influential in the colonization of mineral substrata by algae.

3.3. Heterogeneity of colonization

Results from the settlement studies suggested that aggregation was occurring within and between morphotypes. This had been observed visually and was confirmed by the variation in percentage cover detected throughout a 25-cm square quadrat of fines in the center of a frost polygon at Jane Col (Table 4). The range of % cover (colonization) was considerable and was parallelled by the range in total length per unit area (mesh

Table 4. Heterogeneity of colonization of fellfield polygon fines at Jane Col. TV image analysis of microbial percentage cover, total microbial cell area, and length per unit area.

Parameter	Mean	95% Confidence limits	Maximum	Minimum
Total cover (%)	2.37	±0.64	6.26	0.46
Total length (μm mm^{-2})	6202	±1366	11989	1724
Cell breadth* (μm)	15.0	±0.8	18.8	11.2

* Cell breadth is exaggerated by the TVIA resolution at low magnification. The mean cell breadth (±95% confidence limits) as indicated by selective thresholding and confirmed at higher magnificantion was 8.2±1.0 μm (range 3.8–12.3).

density of filaments). Cell breadth, however, remained relatively constant representing a cyanobacterial population dominated, under the conditions prevailing, by broad long trichomatous filaments. These predominantly fluoresced gold in blue incident light, indicating a high phycoerythrin content in addition to the orange-red fluorescence of phycocyanin under green light.

3.4. Effect of enhanced growth conditions in cloches

The relatively sparse cover of cyanobacteria, frequently dominated by filaments which were often aggregated into "rafts", provided a reservoir of colonizers potentially responsive to improved growth conditions. These included elevated temperature, extended growing season, prolonged humidity, and nutrient enrichment such as carbon and nitrogen from snow algae and moss debris and minerals from precipitation, meltwater and sea spray.

During the two midsummer months, the fellfield fines moisture content was found to be $15.4 \pm 0.2\%$ dry weight ($n=25$) which was $>75\%$ WHC. On inspection of the cloches throughout the summer of 1984–1985 and 1987–1988, the soil surface always appeared dark, indicating moistness. This contrasted with the very light coloration observed occasionally in Petri dish sample plots of the enrichment experiments which were physically isolated from the soil capillary water supply. This relatively constant capillary water supply in the flat topography of this maritime site was replenished throughout the summer by substantial precipitation. Water was therefore unlikely to be growth-limiting for prolonged periods of time at this maritime site.

The stimulatory influence of nutrients has already been demonstrated, but the effect of elevated temperature under field conditions (simulating the global warming of the "greenhouse effect") was unknown. The stimulatory effect of a cloche on cyanobacterial/algal filament development was dramatic (Table 5). The adjacent control quadrat was colonized by filaments and trichomes to an extent similar to the previous experiment, but the cyanobacterial/algal density increased *ca.* 14-fold from *ca.* 5% to *ca.* 74%. This change was accompanied by a 3.2°C elevation in mean ground temperature due to retention of thermal energy derived from natural solar irradiation. Con-

Table 5. The response of algal/cyanobacterial colonizers of fellfield soil polygon fines dominated by filamentous cyanobacteria to warmer environmental conditions in a plastic cloche located for 3 years at Jane Col, Signy Island, relative to an adjacent exposed control site. Data obtained by EFTVIA.

Variable	Mean±SD		Mean difference	% change
	Control	Cloche**		
Temperature (°C)*	4.4±1.2	7.6±1.7	3.2	+73
Area colonized (%)	4.8±1.5	73.9±8.0	69.1	+1440
Total length of cells ($\mu m \times 10^{-3}$ mm^{-2})	3.9±2.0	17.9±7.4	14.0	+358
Cell length (μm)	25.3±1.7	78.0±45.2	52.7	+208
Cell breadth (μm)	10.2±1.6	7.1±0.9	−3.1	−30
Cell volume (μm^3)	1641±479	4719±3744	3078	+188

* Integrated surface temperatures (January–March, 1988).

** All values are significantly different from the controls ($P<0.05$).

ditions in the cloche also stimulated both the total and mean length of the colonizers and their mean unicell/trichome volume. However, their mean breadth decreased concurrently, reflecting an increasing predominance of long trichomatous filaments as the primary response of the initial population.

4. Conclusion and Discussion

The experiments summarized here represent a progressive investigation of the interactions between the surface texture of the fellfield fines substratum, its nutritional status, and microclimatic conditions at the soil surface and the development of cyanobacterial and algal communities in some frost polygons at Signy Island.

The findings suggest that the habitat was probably not seriously N-limited but was more likely to be periodically C-limited, alternating with flushes of abundant soluble carbon derived from frost-damaged cryptogamic cells (TEARLE, 1987).

Cells and trichomes which were translocated in meltwater were not exclusively dependent on grains of a particular size for their retention, although settlement by filaments was apparently associated more frequently with a substratum composed of grains having *ca.* 75 μm side length. Inconsistencies in the settlement of mineral substrata indicated that the formation of "rafts" composed of filamentous mesh embedded with unicells in a mucilagenous matrix was obscuring the responses of individual cells and trichomes. This rafting led to heterogeneity in the distribution of cyanobacterial and algal colonizers on the flat, apparently homogeneous, fines in the center of the polygons.

The potential for population expansion over the soil surface was apparent, and was triggered by exaggerating some of the natural growth-promoting microclimatic parameters *in situ* by means of a cloche. Mean surface temperature and humidity were elevated, resulting in a large increase in microfloral cover.

The oceanic influence on this poorly-drained maritime Antarctic site makes water limitation on a large scale a rare occurrence. However, microbes live in microenvironments so that the osmotic stress of desiccation may be significant on a local scale whilst not having a profound influence on the whole ecosystem. Colonization is, however, a local event. Where there are large numbers of incident propagules, or where a propagule bank has accumulated over a prolonged period of time, such localized effects may be of limited importance because of the statistical likelihood of sufficient propagules occurring in the pockets of habitat favorable for growth (see Fig. 2). WYNN-WILLIAMS (1986) has summarized the main requirements for potential microbial colonizers. He emphasized the difference in the importance of available water in the maritime and continental Antarctic. Continental cold desert conditions may have water activity as low as 0.48, below the minimum value of 0.6 required for microbial growth (HOROWITZ, 1979). It was therefore not surprising that water did not stimulate colonization at Jane Col as the soil profile provided adequate moisture to compensate for the periodic drying of the soil crust. Cracking of the crust during desiccation may, however, have a damaging effect on microbial crust integrity which may partly account for the prevalence of "rafts" (WYNN-WILLIAMS, 1985). The slight stimulatory effect of nitrogen indicated potential growth-limitation by dissolved N, but GREENFIELD (1989) has shown that N is available

in various forms at Jane Col, including ammonia. It is likely that snow accumulates N from the atmosphere and latterly from the growth of snow algae during the winter and early spring and deposits it on the soil surface in meltwater.

The availability of dissolved organic carbon (DOC) is, however, more critical as shown by the enrichment study. The influence of DOC on algae and cyanobacteria is potentially both direct and indirect. The binding of the soil crust by mucilages is important for the integrity of the microhabitat. Mucopolysaccharide mucilages have a high C content. Moreover, the osmotic stresses on the microbiota due to desiccation, freezing and salt accumulation result in a need for C-based compatible solutes to protect their membranes (RUSSELL, 1990). Moss extract was most stimulatory for colonization, and TEARLE (1987) has shown that it contains large amounts of polyols and sugars which not only provide energy and C for heterotrophic growth, but also confer cryoprotection (see WYNN-WILLIAMS, 1986). TEARLE (1987) also showed that fellfield soil water from mosses and lichens which have experienced freeze-thaw damage can have a sugar plus polyol content of up to 1.5%. The experimental enrichments here simulated the C-release occurring under these conditions and confirmed its stimulatory effect on colonization processes.

Inorganic enrichments did not have a stimulatory effect as was expected from soil analyses which did not indicate any serious natural deficiencies for microbial growth (HOLDGATE *et al.*, 1967). Sea spray was frequently blown over the Col despite its altitude. Moreover, the experiment was carried out during the midsummer when inorganic nutrients were unlikely to be depleted by prolonged microbial growth.

Micro-organisms adhere to their substrata for a variety of reasons, including stability, protection, exploitation of the flow of nutrient-bearing water, and to obtain nutrients concentrated by adsorption. The findings here, however, suggest that although the length of filaments and trichomes may affect the ability of colonizers to settle on the substratum from flowing water, there are other cell attributes, especially the ability of fellfield algae and cyanobacteria to produce mucilaginous sheaths (WALSBY, 1968; HÄDER, 1987) which act as an adhesive which is more influential than morphology (DAVEY *et al.*, 1990). It is the combination of the mesh of filaments and the mucilagenous matrix which forms the rafts which probably act as integrated inocula on freshly exposed mineral soil after the disruption of frost heave in spring. At this time, meltwater is plentiful and may translocate rafts and propagules for considerable distances, particularly from the icecap which influences the periphery of the fellfield site. Microbial rafts are common in late winter/early spring snow.

The dominant family in fellfield aggregates is the Oscillatoriaceae (Cyanobacteria), especially the genus *Phormidium*. This genus has various morphotypes (BROADY, 1979; BROADY *et al.*, 1984) with trichomes ranging in diameter from 2 to 9 μm. In the enriched polygon, the melt stream used for settlement studies and the polygon used to assess heterogeneity of colonization, the dominant species was *P. autumnale* with broad trichomes up to 9 μm or more (WYNN-WILLIAMS, 1985, 1986). These trichomes were readily recognizable because of their phycoerythrin content and were easily imaged for TV analysis at low magnification, thereby minimizing problems with depth of focus (WYNN-WILLIAMS, 1989a). They were a valuable biological marker for study in a mixed population.

Despite the appearance of a relatively homogeneous soil crust, the microflora of patterned fellfield is heterogeneous at two levels. Firstly, each polygon has a distinct microflora and may be dominated by different species with quite different morphology, such as compact mucilagenous ovoid masses of *Nostoc* sp. or the gently curved filaments of *Phormidium autumnale* described earlier. Each makes a different contribution to soil crust stability. Secondly, there is heterogeneity within a polygon. The variation in density of algal and cyanobacterial colonizers on the soil surface is consistent with the observed prevalence of rafts and the importance of filaments in their structure (WYNN-WILLIAMS, 1989a). The crust is best considered as a mosaic of rafts which probably retain most of their integrity during frost heave and can therefore re-establish themselves quickly after the thaw.

The mean temperature elevation in the cloches is in the range predicted for global warming by the year 2050, especially allowing for an enhancement of the effect at the poles. The middle scenario rate having an increase of 0.3°C per decade predicts global warming of +1.8°C, reduced to +0.9 to +1.3°C in summer but enhanced to +3.6 to +4.3°C in winter (WORLD METEOROLOGICAL ORGANIZATION, 1988). If the thermal effect is the dominant factor enhancing cyanobacterial colonization in the cloche, the community escalation over three years is probably an underestimate of potential development. As in oceanic and freshwater ecosystems, the phototrophs of the exposed soil crust are sensitive indicators of global warming.

Although elevated temperature and stable humidity were probably the major factors enhancing cyanobacterial growth in the cloches, other factors were probably contributory. The elevated temperature will result in an extension of the growing season and a reduction in the number of potentially disruptive freeze-thaw cycles. The plastic of the cloches is known to screen out a high proportion of biologically harmful solar Ultraviolet-B (UV-B) radiation whilst transmitting photosynthetically active radiation (PAR) (R. I. LEWIS SMITH, pers. commun.). UV-B is known to inhibit photosynthesis (WORREST *et al.*, 1981; HÄDER, 1986; EL-SAYED and STEPHENS, 1990) and photosensory behavior (HÄDER, 1987) in algae and cyanobacteria including *Phormidium* species (HÄDER, 1984). This environmental stress may even result in changing population composition because of differential sensitivity to the radiation. Cyanobacteria are especially vulnerable as they are typically low-light organisms whose photosynthetic pigments are photooxidized at high-light intensities (WALSBY, 1968; WYNN-WILLIAMS, 1989b). Their occurrence on the surface crust of soil is therefore paradoxical, and their survival may depend on mutual shading. Their sensitivity and accessibility make them valuable indicators of changing UV-B irradiation as the 'ozone hole' expands over Antarctica.

Despite the integrity of the self-contained 'rafts', their interconnections are vulnerable to physical disruption. The cloche shelters the soil from the physical impact of raindrops and wind abrasion, thereby permitting better integration of the cyanobacterial mesh over the soil surface and preventing the loss of colonizers from the system. However, it also restricts the introduction of fresh propagules and airborne particulate nutrients to those which penetrate the small vents. Gaseous nutrients may enter more freely, although gas exchange will nevertheless be restricted by reduced mixing and turbulence. This will also result in an altered O_2/CO_2 balance relative to the unenclosed control.

The biomass resulting from the enhanced cyanobacterial colonization will not only add C and N to the otherwise periodically oligotrophic environment but will also produce a structured, food-rich microhabitat for grazers such as protozoa (COWLING and SMITH, 1986) and nematodes (PICKUP, 1988).

The relatively low species diversity and the well-defined naturally sorted particles of fellfield frost-polygon fines provide a natural laboratory for testing the response of the microflora to environmental change. Not only can this ecosystem be monitored in the field, but relatively undisturbed cores of soil crust can be put in microcosms under controlled conditions to determine visually and physiologically the primary influential factors. Moreover, the autofluorescence of cyanobacteria and algae prevents disruption of the natural community by staining. The polygon ecosystem is eminently suitable for studies of local 'island' biogeography, propagule banks, and the aerobiology of their inocula as envisaged in the international BIOTAS programme (Biological Investigation of Terrestrial Antarctic Systems) of SCAR (Scientific Committee on Antarctic Research).

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