

## **A Statistical Analysis of the Relationships Among Viable Microbial Populations, Vegetation, and Environment in a Subantarctic Tundra**

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**Abstract.** Parametric and nonparametric analyses were used to investigate the relationships between the populations of viable microbes and 4 edaphic variables—soil moisture, rainfall, temperature, and pH. Microbial populations were sampled over a 2-year period in contrasting grass and moss stands on the subantarctic island of South Georgia. Moisture was found to be the most significant edaphic variable, but there were highly significant correlations between bacterial and fungal populations at both sites. Individual plant species showed clear correlations with both bacterial and fungal populations.

### **Introduction**

Changes in the microbial biomass of a tundra ecosystem have important effects on nutrient availability, both for plants and soil organisms. There has been only limited, and mainly qualitative, examination of the relationships between edaphic factors and seasonal estimates of tundra microbial populations and of how substrate quality might affect these.

There appear to be few studies incorporating both statistical analyses and long-term sampling of both microbial populations and environmental variables. The most detailed study [12] attempted a number of analyses to link viable bacterial counts from the litter of 34 International Biological Programme (IBP) tundra sites with physical and chemical characteristics of the soil and with selected vegetation and climate factors. The regressions on site component values suggested that the aerobic viable count was related exponentially to available calcium, phosphorus, pH, and the quality of soil organic matter. A similar study on fungi [8] used a correlation matrix to determine the importance of 11 environmental parameters on fungal mycelial length from 21 IBP sites from polar to temperate moorland. Again pH and organic matter content were found to be the most important factors, together with the addition of moisture.

The range and variety of sites encompassed by the IBP Tundra Biome studies were so great that synthesis of the data was possible only at a gross scale. At a more detailed level, the microbiological [11] and decomposition [10] syntheses were also limited by the diversity and complexity of the available data sets.

The subantarctic island of South Georgia, considered by IBP as southern tundra, has a sufficiently limited flora and fauna to make quantitative investigations of ecological interactions feasible. Within close proximity, there exist quite distinct ecological niches characterized by few species.

As part of studies of decomposition rates and processes on South Georgia [19], extensive data on the microbial populations of sites with contrasting vegetations, together with detailed microclimate and edaphic information, were collected at frequent intervals over a long experimental period. These data permit a statistical analysis of the relationships among the microbial populations, the local vegetation, and a number of edaphic factors at a local rather than global level.

## Methods

### Introduction

South Georgia (54°17'S, 36°30'W) lies south of the Antarctic Convergence; it is a mountainous island with an extensive ice cap and glaciers. The climate is cool oceanic, and a range of soil types have developed [22]. In sheltered areas at sea level, minimum air temperatures rarely fall below -5°C in the summer or below -15°C in the winter. Grassland litter temperatures in sheltered north-facing sites can reach 40°C in summer. There is little seasonal variation in the annual precipitation of c. 1,400 mm, although rain is more frequent than snow in summer. The most sheltered areas of the island lie around Cumberland and Stromness bays on the northeast coast. The phanerogamic flora is limited to 25 species [9], but the cryptogamic flora is more diverse with over 400 species.

### Sites

Two contrasting areas of vegetation and soil, without permafrost and unaffected by any grazing or human activities, were selected for study in the Maiviken area of Cumberland Bay. At each study area 100 marked quadrats, each 1 m<sup>2</sup>, were available for sampling. Mean vegetation cover was assessed using 200 1-m<sup>2</sup> quadrats at the grassland and 225 1-m<sup>2</sup> quadrats at the mossbank (Table 1).

The grassland site is located on the shallow southwest-facing slope beside a lake at about 90 m above sea level and 0.5 km inland. The site is well drained with a brown earth soil type, the most highly developed on the island. This grass heath formation, the climax vegetation on such soils [9], is dominated by *Festuca contracta* T. Kirk. The cryptogamic component consists mainly of the mosses *Chorisodontium aciphyllum* (Hook. f. et Wils.) Broth. and *Polytrichum alpinum* Hedw., and several species of lichen, chiefly of *Cladonia*, are also frequent. The litter layer is variable but normally 5–8 cm deep.

In contrast, the mossbank site is a deep "raised bog," overlying about 2 m of ombrogenous mesotrophic peat [21], which had developed between low hills 10 m above sea level. The mossbank is formed by 2 tall turf-forming mosses, the dominant *Polytrichum alpestre* Hoppe and *Chorisodontium aciphyllum*, with frequent liverworts. Some lichens, chiefly *Cladonia* spp., and the short rush *Juncus scheuchzerioides* Gaudich. are frequent associates. This community, but without a phanerogamic component, is also found in the maritime Antarctic [20]. The soil has a low water table but comparatively high water content.

**Table 1.** Mean percentage vegetation cover at the grassland and mossbank

Species	Mean cover (%)
Grassland species	
<i>Chorisodontium aciphyllum</i>	68 ± 8
<i>Festuca contracta</i>	40 ± 34
<i>Cladonia rangiferina</i>	15 ± 8
<i>Polytrichum alpinum</i>	7 ± 5
<i>Acaena magellanica</i>	3 ± 3
<i>Phleum alpinum</i>	3 ± 4
Liverworts	5
Other lichens	5
<i>Rostkovia magellanica</i>	1-2
Mossbank species	
<i>Polytrichum alpestre</i>	68 ± 14
<i>Juncus scheuchzerioides</i>	23 ± 9
<i>Chorisodontium aciphyllum</i>	21 ± 9
Liverworts	5
Lichens	5

### Microbiology

At monthly intervals, from February 1977 to December 1978, one core (38 mm diameter, 250 mm long) was removed from each of 8 numbered quadrats chosen by using random number tables for each site. Three from each site were used for microbiological investigation and the remainder for pH and moisture content determinations. On each sampling occasion the percentage cover of each species in the vegetation at the surface of each core (11 cm<sup>2</sup>) was estimated.

Sterile instruments were used to obtain approximately 1-g field samples from the center of the 0-2, 6-8, and 12-14 cm levels of each core. After weighing, each sample was homogenized in an MSE homogenizer with 99 ml of sterile 0.25 strength Ringer solution for 3 min at c. 10,000 rpm. Further dilutions (10<sup>-3</sup> and 10<sup>-4</sup>) were made, and 0.1 ml aliquots of these were surface-spread onto triplicate agar plates for viable counts of bacteria and fungi. The surface-spread method was used in preference to the pour-plate method to reduce possible temperature stress to any psychrotrophic organisms that were present [1]. Counts of fungal colony-forming units (CFU) were made after 10 days incubation at 10°C on Czapek-Dox agar with aureomycin to inhibit bacteria. Counts of bacterial CFU were made after 15 days incubation at 10°C in one-tenth strength Tryptone-Soya agar (Oxoid, 50 mg l<sup>-1</sup>) with Actidione (Upjohn, 50 mg l<sup>-1</sup>) to inhibit fungi.

Mean monthly aerobic bacterial and fungal CFU counts at 3 depths on each site were derived from 3 core values, each of which was the mean of triplicate plates. Each core mean was converted to numbers g<sup>-1</sup> dry wt soil and then transformed to a log<sub>10</sub> basis. The site mean and standard deviation were thus obtained as mean and standard deviation of the 3 log<sub>10</sub> values. As each collection yielded some cores with exceptionally large microbial populations, the data were clearly not normally distributed, and each core was therefore treated as a population and was transformed before analysis.

Following the removal of aliquots for plate counts, 1 ml of 10<sup>-2</sup> dilution was used to make Jones and Mollison [13] slides for total counts. Numbers of microscopic fields to be counted per slide were assessed by determining standard error as a percentage of the mean. Forty fields were used, and 39 samples were counted.

### *Edaphic Variables*

*Moisture.* The total water content of each soil level sampled from each site was determined in triplicate by drying at 60°C for a month. Moisture content was calculated as a percentage of the fresh weight.

*pH.* The pH of the 3 levels from each site was measured monthly on a homogenized slurry in distilled water. Initially a nonstandard soil/water ratio of approximately 1:9 by volume was necessary in order to macerate dry summer cores from the mossbank. After May 1978, slightly larger cores gave a ratio of 1:6. This change in dilution ratio may have made the pH at most 0.2 units more acid on some occasions but this was well within the standard errors for monthly means.

*Temperature.* Air and soil temperatures were monitored using permanently positioned thermistors (Gulton 32TD 25) in an automatic micrometeorological data logging system. A statistical comparison of data from the 2 sites over 11 days showed sufficiently close similarities to permit the more complete data set from the grassland to be applied to both sites. Thermistor probes in the litter layer and in the soil (−5 and −10 cm) measured temperatures every 5 min with an accuracy of ±0.5°C up to 20°C, falling to ±1°C at 40°C. To simplify usage of this large data set, readings at 00, 03, 06, 09, 12, 15, 18, and 2100 hours local time were abstracted and this information divided into 10-day periods. The absolute maximum, mean daily maximum, overall daily mean, mean daily minimum, and absolute minimum temperatures for each of these periods were then calculated.

*Rainfall.* Daily summer rainfall measurements were taken from a standard rain gauge at Grytviken, approximately 5 km from the grassland site. Winter measurements were derived from snow equivalents.

### *Data Analysis*

Data files were assembled from the microbial and edaphic data recorded for each depth at both sites for each of the 23 monthly samples. These are described below, together with the abbreviations used in subsequent sections:

1. The mean  $\log_{10}$  transformation of the viable bacterial numbers of triplicate monthly samples (as viable bacteria  $g^{-1}$  dry wt soil)—LOGBACT.
2. The mean  $\log_{10}$  transformation of the number of viable fungal propagules of triplicate monthly samples (as fungal propagules  $g^{-1}$  dry wt soil)—LOGFUNG.
3. The mean/variance ratio of the transformed bacterial and fungal data—M/V BACT and M/V FUNG.
4. Three depths (0–2, 6–8, and 12–14 cm) at each site—DEPTH.
5. The moisture present as a percentage of the fresh weight—% MOISTURE.
6. The pH of the sample profile—PH.
7. Precipitation (mm) in the 2-, 10-, and 30-day periods prior to sampling—RAIN 2, RAIN 10, and RAIN 30.
8. At each of the 3 sampling depths, the absolute maximum and minimum temperatures (°C) of the soil in the 10-day period prior to sampling—ABSMAX and ABSMIN.
9. At each of the 3 sampling depths the mean daily maximum and minimum temperatures (°C) of the soil in the 10-day period prior to sampling—MEANMAX and MEANMIN.
10. At each of the 3 sampling depths the overall mean temperature (°C) of the soil in the 10-day period prior to sampling—MEAN.
11. Files were created which contained the date, site, viable microbial numbers at 0–2, 6–8, and 12–14 cm depths, and the relative percentages of the major vegetation types present at the surface of each core.

Several parametric analytical methods were used, from the Statistical Package for the Social Sciences (SPSS) [24], to relate the microbial populations to the edaphic variables. Bivariate correlation analyses were used to examine the relationships between pairs of variables, and their statistical significance was assessed using Pearson correlation coefficients. As the vegetation data from the cores were not normally distributed, nonparametric correlation analysis was used.

Stepwise multiple regression analysis was also used for data from each site. In this, the independent variable accounting for the greatest amount of variance of the dependent variable was entered first, then that which, in conjunction with the first, explained the greatest variance, and so on. The significance of each variance ratio could then be assessed.

## Results

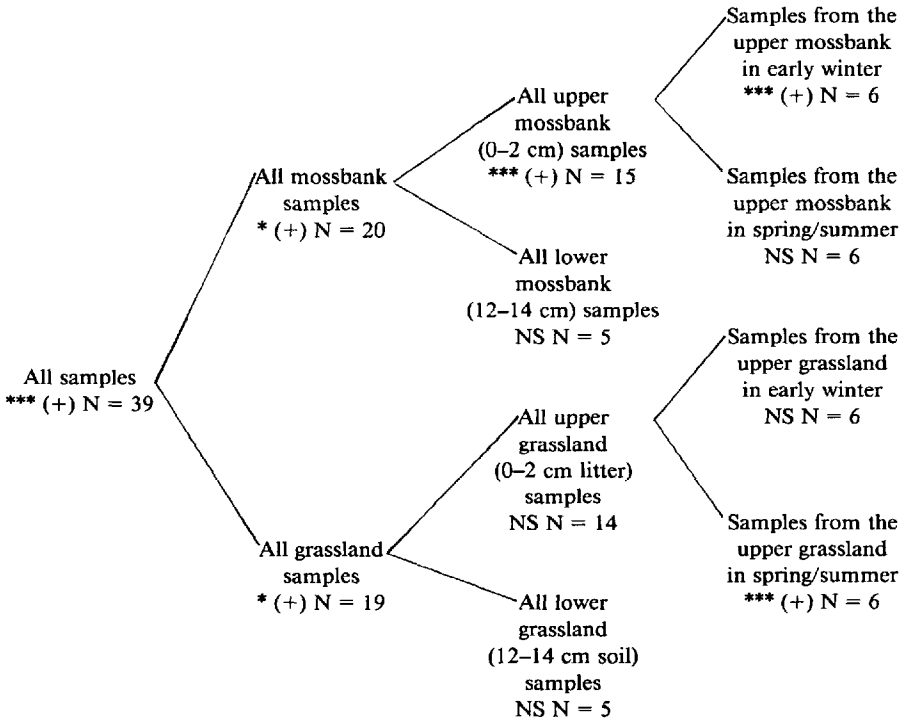
The mean total number of bacteria in all the 39 samples counted was  $5.04 \times 10^{11} \text{ g}^{-1}$  (range  $0.94 \times 10^{11}$ – $10.6 \times 10^{11}$ ). Comparisons of the viable and total counts for samples from the upper horizons at both sites showed the total count to be about  $10^4 \text{ g}^{-1}$  greater. A correlation analysis between total and viable bacterial counts at each site (Fig. 1) showed that all significant correlations were positive. The pattern of significance appears difficult to explain with contrary seasonal effects at the upper levels of the 2 sites. Although sample sizes for some categories were small, this is not necessarily the reason for a lack of correlation.

In the first comparison between the viable microbial populations and all the edaphic variables (Table 2), depth was considered as a separate independent variable, allowing data from all 3 depths to be used for all correlations. Table 3 provides additional information on the relative importance of depth at each site from further bivariate correlation analyses.

At the grassland, LOGBACT and LOGFUNG both decrease significantly with depth but increase with moisture. The decrease in both moisture (Table 3) and organic matter with depth (Table 4) supports the hypothesis that increased microbial numbers are associated with increased total organic matter and/or increased moisture. The decrease in the mean/variance ratio of the bacteria with increasing depth at the grassland (Table 3) may also be associated with increased mineralization and a decrease in favorable microhabitats, leading to the sampling of a more homogeneous population with depth.

A similar relationship is not, however, seen at the mossbank. While % MOISTURE shows a significant increase with depth (Table 3) and the amount of organic material present does not alter appreciably (Table 4), bacterial numbers show a significant decrease with depth (Table 2). Fungal numbers show no correlation with depth. This may reflect the mycelial growth pattern which can occupy both the horizontal and vertical interstices among the moss shoots with equal facility. The absence of a significant relationship between LOGBACT and LOGFUNG and % MOISTURE at this site suggests that sufficient moisture was available at all depths, even during the summer, because of the ability of the peat to retain water. At the grassland, close relationships between both LOGBACT and LOGFUNG and % MOISTURE, as well as the decrease in moisture with depth, would suggest the likelihood of higher microbial numbers in the upper levels (Table 2).

In order to see whether there might be an association between LOGBACT



Where: N = Number of cases  
(+) or (-) = Sign of correlation coefficient where significant

Significance of correlation coefficient  
 \*\*\* =  $P < 0.001$   
 \*\* =  $P > 0.001 < 0.01$   
 \* =  $P > 0.01 < 0.05$   
 NS =  $P > 0.05$  (Not significant)

Fig. 1. Results of the correlation analysis between the total and viable bacterial populations

and LOGFUNG, a correlation for the 2 for all depths at each site was carried out. This showed a highly significant positive correlation ( $P < 0.01$ ) between the 2 at the mossbank and a very highly significant positive correlation ( $P < 0.001$ ) at the grassland. Further evidence is necessary to establish if this is a real association, since both fungi and bacteria might only be responding in a similar fashion to an environmental change.

At the grassland, both bacterial and fungal populations increase with increasing pH. The ranges of pH at the sites were 3.5–4.5 in the mossbank and 4.0–5.2 in the grassland, similar to those given by Smith and Walton [22] for comparable soil types. While in general, bacteria grow better at a pH nearer neutrality, fungi are usually associated with acid conditions. The positive correlation between fungi and pH at the mossbank cannot be explained in this way, as pH did not alter significantly with depth, and moisture increased significantly with depth (Table 3).

At the grassland, the increase in the numbers of microorganisms with decreasing temperatures (Table 2) may be due to higher moisture retention at

Table 2. The statistical significance of the correlation between viable microbial numbers and edaphic variables

	% MOISTURE										
	DEPTH	RAIN 2	RAIN 10	RAIN 30	ABS-MAX	MEAN-MAX	MEAN	MEAN-MIN	ABS-MIN		
Grassland	LOGBACT	***	***	NS	NS	NS	NS	*	***	***	
	LOGFUNG	-	+	NS	NS	NS	*	*	-	**	
Mossbank	LOGBACT	***	NS	NS	NS	NS	NS	NS	*	**	
	LOGFUNG	-	+	*	*	NS	NS	NS	-	-	

Sign of correlation: given as + or - only if it is significant. Sample number of each site = 22  
 Statistical significance of correlation coefficients:  $P < 0.001 = ***$ ;  $P < 0.01 = **$ ;  $P < 0.05 = *$ ;  $P > 0.05 = NS$  (not significant)

**Table 3.** The significance of the correlations between increasing depth, microbial numbers, and 2 edaphic variables at the sites

	LOG- BACT	M/V BACT	LOG- FUNG	M/V FUNG	% MOIS- TURE	PH
Increase in depth at the grassland	***	***	***	NS	***	*
	-	-	-		-	-
Increase in depth at the mossbank	***	NS	NS	NS	***	NS
	-				+	

Sign of correlation: given as + or - only if it is significant. Sample number at each site = 22

Statistical significance of correlation coefficients:  $P < 0.001 = ***$ ;  $P < 0.01 = **$ ;  $P < 0.05 = *$ ;  $P > 0.05 = NS$  (not significant)

**Table 4.** Organic content of soil or litter components at each site

Site	Depth/material	Loss on ignition (% of oven dry wt)
Mossbank	0-3 cm	95.0
	3-6 cm	96.2
	6-9 cm	97.5
	9-12 cm	96.6
Grassland	<i>Festuca</i> culms	91.9
	Green upper moss (0-2 cm)	92.5
	Brown lower moss (2-5 cm)	86.5
	Organic/mineral horizon (5-7 cm)	69.8
	Top of mineral layer (7-10 cm)	45.8
	Mineral soil (below 10 cm)	13.0

lower temperatures. At the mossbank, only the bacteria seem to follow a similar, though less significant, trend. As moisture is apparently not a significant influence at this site, such a relationship might reflect a true temperature response. The measures of rainfall used were apparently not an important factor in microbial population changes at either site, and only an increase in precipitation 2-10 days before sampling showed a significant correlation with fungi at the mossbank (Table 2).

LOGBACT and LOGFUNG were incorporated as the dependent variables in a multiple regression analysis against all other factors (including the microbial population not designated dependent) (Table 5). The results of these regression analyses and the bivariate correlations are similar but not the same, because regression analysis considers the additive function of the variables rather than simple association. At the grassland, the only 3 significant factors associated with LOGBACT were, in order of significance, LOGFUNG, DEPTH, and ABSMIN. Fungi at this site were influenced significantly by 2 variables—LOGBACT and % MOISTURE. In the mossbank, only DEPTH and LOGFUNG (in that order) were associated with bacteria, while RAIN 30 and LOG-



**Table 5.** Stepwise multiple regression analysis of LOGBACT and LOGFUNG at all depths

	Dependent variable	Ranked independent variables	Significance of the variance ratio
Grassland	LOGBACT	1. LOGFUNG	0.1%
		2. DEPTH	0.1%
		3. ABSMIN	1.0%
		4. RAIN 2	NS
	LOGFUNG	1. LOGBACT	0.1%
		2. % MOISTURE	1.0%
3. RAIN 10		NS	
Mossbank	LOGBACT	1. DEPTH	0.1%
		2. LOGFUNG	5.0%
		3. % MOISTURE	NS
	LOGFUNG	1. RAIN 30	1.0%
		2. LOGBACT	5.0%
		3. RAIN 2	NS

BACT were the only factors associated with the fungi. These analyses support the correlations in Table 2, with the addition of RAIN 30 at the mossbank and omission of % MOISTURE at the grassland.

Further analysis without the independent microbial variable and omitting the 5% level of significance established % MOISTURE as the only independent variable of any significance ( $P < 0.1\%$ ) for both bacteria and fungi at the grassland. At the mossbank, only RAIN 30 continued to show a significant relationship with fungi. Division of the data by depth before analysis gave no further correlations for the mossbank site. However, subdivision by depth at the grassland showed both the importance of moisture to bacteria and fungi at the intermediate depth and that temperature (ABSMAX and MEANMAX) was of some significance ( $P < 1.0\%$ ) to both groups at greater depth.

Some of the monthly changes in the viable bacterial and fungal populations may be explained by the edaphic variations described. However, since much variation could not be accounted for by these variables, the relationship to primary resource quality [23] was considered. The principle feature affecting this was considered to be the plants growing at each site (Table 1) since they contributed to available microbial resources both from material input at the soil surface and within the soil matrix from roots and rhizomes.

The nonparametric bivariate correlation analyses between vegetation and microbial numbers at the grassland (Table 6) showed that the viable bacterial population of the litter layer (0–2 cm) increased as the proportion of the grass *Festuca* increased and decreased as the proportion of the moss *Chorisodontium* increased. The only other correlations were at depth. There bacterial populations showed a marked decrease with high proportions of the moss *Polytrichum alpinum*, and there were slight positive associations between bacteria and the rush *Rostkovia* and between fungi and *Chorisodontium*.

In the mossbank, high bacterial populations were associated with the rush

**Table 6.** Nonparametric bivariate correlation analysis of microbial populations with vegetation cover at both sites

Grassland	Depth (cm)	<i>Festuca contracta</i>	<i>Rostkovia magellanica</i>	<i>Polytrichum alpinum</i>	<i>Chorisodontium aciphyllum</i>
Viable bacteria	0-2	***	NS	NS	***
		+			-
	6-8	NS	NS	NS	NS
	12-14	NS	*	**	NS
			+	-	
Viable fungal propagules	0-2	NS	NS	NS	NS
	6-8	NS	NS	NS	NS
	12-14	NS	NS	NS	*
					+

Mossbank	Depth (cm)	<i>Juncus scheuchzerioides</i>	<i>Polytrichum alpestre</i>	<i>Chorisodontium aciphyllum</i>
Viable bacteria	0-2	***	***	**
		+	-	+
	6-8	***	*	NS
		+	-	
	12-14	NS	NS	NS
Viable fungal propagules	0-2	NS	*	NS
	6-8	NS	*	**
			-	+
	12-14	NS	*	***
			-	+

The significance of the Spearman correlation coefficient shown as: \*\*\* =  $P < 0.001$ ; \*\* =  $P < 0.01$ ; \* =  $P < 0.05$ ; NS =  $P > 0.05$  (not significant)

The sign of the correlation coefficient is shown if  $P < 0.05$

Sample number at each site = 66

*Juncus* and to a lesser extent with *Chorisodontium*. Low bacterial populations were found in cores with high *Polytrichum alpestre* contents, and this was also true for fungal populations. High fungal populations were found in *Chorisodontium*-dominated cores, but *Juncus* had apparently no significant effect on viable fungal numbers.

## Discussion

So that the present analyses could be seen in a wider context, a comparison was made with numbers of organisms at other tundra sites using the monthly means for viable bacteria and fungi [18]. Comparison of the mean total bacterial counts from the upper levels at both sites with other tundra data [15] shows the South Georgian figure to be high ( $10^{11}$  compared with  $10^9$   $g^{-1}$ ) but comparable to data obtained from a wet tundra meadow at Barrow [5] and a

**Table 7.** The mineral content of principal plant species of the grassland and mossbank (adapted from Walton and Smith [25])

		Total (% of dry wt)						
		Na	K	Ca	Mg	P	N	Ash
Grassland								
<i>C. aciphyllum</i>		0.07	0.54	0.30	0.21	0.20	1.03	3.64
<i>F. contracta</i>	Leaf litter	0.02	0.20	0.16	0.11	0.06	0.65	3.43
	Live leaves	0.01	1.60	0.09	0.09	0.21	1.44	4.27
Mossbank								
<i>J. scheuchzerioides</i>		0.34	3.38	0.46	0.21	0.34	2.38	9.14
<i>P. alpestre</i>		0.06	0.66	0.50	0.15	0.12	1.20	2.03

Norwegian wet meadow [7]. The ratio of viable to total counts falls within the range discussed by Bunnell et al. [5].

In the complex ecosystem of a soil, it is difficult to relate cause and effect directly in the interactions between biological and environmental variables. In assessing the relationship between moisture and microbial populations on South Georgia, precipitation, soil humidity, total soil water, and suction pressure were all potential parameters. Correlations were found with both measured parameters (precipitation and total soil moisture), but these are likely to be only partial explanations. The different moisture trends with depth at the 2 sites (increasing at the mossbank, decreasing at the grassland) were apparently of less importance than the absolute amounts of water present. It may be for this reason that RAIN 30, with the longest time period of any of the variables used, was only significant at the mossbank—the wetter site.

Soil moisture, measured in various ways, has been reported as a controlling feature in other microbial studies of tundra sites [3, 4, 8]. Temperature has also appeared as an important controlling variable, but most studies have accorded it less significance than moisture [3, 4, 26].

Bissett and Parkinson [2], while studying the distribution of fungi from 3 alpine tundra sites by factorial analysis, noted the strong influence of depth on species diversity. Their parallel study of the functional relationships between soil fungi and environment at the same sites showed temperature, moisture, available potassium, and soil pH to be the most important variables of the 13 studied [3]. Computer model investigations of the response of microbial populations in polar and temperate sites [4] suggested that deeper communities have narrower temperature and moisture ranges than surface communities. This is in good agreement with the present data for moisture. The negative correlations with minimum temperatures suggest that the South Georgian populations are not dominated by psychrophilic species.

The relationships between viable microbial numbers and surface vegetation have not previously been investigated by statistical analysis. At the mossbank, the strong positive association between large microbial populations and the rush *Juncus* may reflect the availability to microbes of some of the nutrients required to sustain the growth of its horizontal rhizomes [6] and lateral assimilatory shoots. A plant as active as *J. scheuchzerioides* may provide an exudate rich in organic and inorganic nutrients. These, together with sloughed off root

cells and an adequate availability of water, should provide a rhizosphere suitable for microbial growth especially of the more immobile bacteria. The availability of nutrients from herbaceous plant roots and tree roots and the association between soil microorganisms and plant roots have been considered by Smith [23] and Parkinson [16], respectively. In contrast, the mosses at this site (Table 7) are relatively nutrient-poor [25]. They contain complex organic compounds such as polyphenols which, if present in leachate, may inhibit microorganisms. They may also possess a waxy cuticle which serves as an active barrier to microbial attack as well as reducing the loss of water and exudates. Such a cuticle is well-developed in *Polytrichum* spp. [16].

The 2 species of *Polytrichum* show different morphological characteristics. *P. alpestre* at the mossbank site has its stems covered in a thick tomentum of rhizoids which are never developed on *P. alpinum* stems to the same degree. These rhizoids are likely to inhibit air movement through the soil profile and facilitate the retention of water. Damage or decay of rhizoids might be expected to produce more leachates from *P. alpestre* than from *P. alpinum* stands.

At the grassland site, only the bacterial population is significantly associated with the vegetation. The grass *Festuca* apparently provides a favorable habitat and the moss *Chorisodontium* an unfavorable one. The lack of correlation between *Polytrichum* and the microbial populations at this site is almost certainly a reflection of the relative frequency of its occurrence with *Chorisodontium* (7% and 68%, respectively, Table 1). At this site, *Festuca* forms a slightly richer nutrient source than the moss (Table 7). The failure of its rhizosphere to provide a favorable habitat deeper in the profile may be due to the decrease in total organic matter and in moisture content with depth.

Although this paper deals specifically with data from a subantarctic tundra area, we suggest that the approach could be used more generally for investigating the complex relationships between microbial populations and their environment.

*Acknowledgments.* We would like to thank the British Antarctic Survey for the opportunity to carry out this work, the BAS personnel on South Georgia between 1976 and 1979 for their encouragement and assistance in the field, and Dr. D. D. Wynn-Williams for his helpful criticism of the manuscript. We are also grateful to Dr. R. I. L. Smith for the data in Table 1.

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