Proc. NIPR Symp. Polar Biol., 3, 120-132, 1990

MICROBIAL ECOLOGY OF SOILS FROM WILKES LAND, ANTARCTICA: II. PATTERNS OF MICROBIAL ACTIVITY AND RELATED ORGANIC AND INORGANIC MATTER

Manfred BÖLTER

Institute for Polar Ecology, University of Kiel, Olshausenstraße 40, D-2300 Kiel 1, F.R.G.

Abstract: Concentrations and distributions of inorganic and organic matter were analyzed in soil samples and on plant material collected near Casey Station, Wilkes Land, during the austral summer of 1985/86. In addition to these parameters a detailed study of the microbial biomass and the bacterial population was carried out by estimating bacterial number and biomass by epifluorescence microscopy. Characteristics of bacterial activity were described by means of enzymatic studies as well as uptake and respiration of ^{14}C labelled glucose. The data show wide variations of individual parameters. A correlation analysis of parameters and samples was carried out, and the correlation matrices were analyzed by different cluster algorithms. The results show significant separations of different groups of parameters and reveal different groupings of samples. They can be described by a set of parameters of which each has a homogeneous distribution. Further, it is possible to distinguish individual groups of samples by parameters with non-overlapping ranges of measurements. The discussion concentrates on the spatial organization of this environment and theoretical aspects of this ecosystem.

1. Introduction

Studies on terrestrial ecology of polar environments concentrate mainly on the Arctic, Subantarctic or the Antarctic deserts (*e.g.*, CAMERON *et al.*, 1970; BROWN *et al.*, 1980; SMITH, 1984, 1985; SMITH, 1988). Some of these studies even enter into rather complex flow models describing seasonal aspects of the system (SMITH, 1988). Multivariate analysis of large data sets from those studies is carried out during the synthesis of the IBP program (HOLDING *et al.*, 1974).

The knowledge on terrestrial ecology with regard to microbial processes in Antarctica, however, is very poor. There are several reasons. Namely, Antarctica presents the most severe conditions for life processes and their study. Also, these ecosystems are widely regarded as dormant systems where "nutrient availability and turnover are limited by low metabolic activity" (SMITH, 1985). This, obviously, is the case in high latitudes where temperature primarily limits the availability of water and, hence, biological processes. The maritime and coastal Antarctic areas, however, have enough time available for favorable conditions to sustain biological processes, *i.e.* primary production and decomposition.

Severe environmental conditions at Wilkes Land are caused by strong winds and

low temperatures but also wide ranges of temperatures due to solar radiation and subsequent heating of surface layers up to 40°C (SMITH, 1986). Small-scale topography due to sheltered areas on the lee of boulders results in a strong patchiness (BÖLTER *et al.*, 1989). Thus it is of interest to analyze these patterns of the systems and their influences on the microbial system by analyzing variabilities of biological and chemical properties of the soils in order to get a better idea of the scales and boundaries of this system.

This paper presents an analysis of data of physical, chemical and biological properties of different soil samples from a fellfield area near Casey Station, Wilkes Land. The data are analyzed by rank-correlation and subsequent cluster analysis of the correlation matrices (R- and Q-mode) with regard to spatial organization and different environmental parameters (BÖLTER *et al.*, 1980). Results are discussed qualitatively with reference to other investigations and with special regard to some theoretical aspects of terrestrial microbial ecology.

2. Materials and Methods

Sampling was carried out during November/December 1985 on a hill near Casey Station, Wilkes Land, approximately 40 m above sea level, 1 km south of the station (Fig. 1). A detailed description of this area is given by SMITH (1986). The total sampling

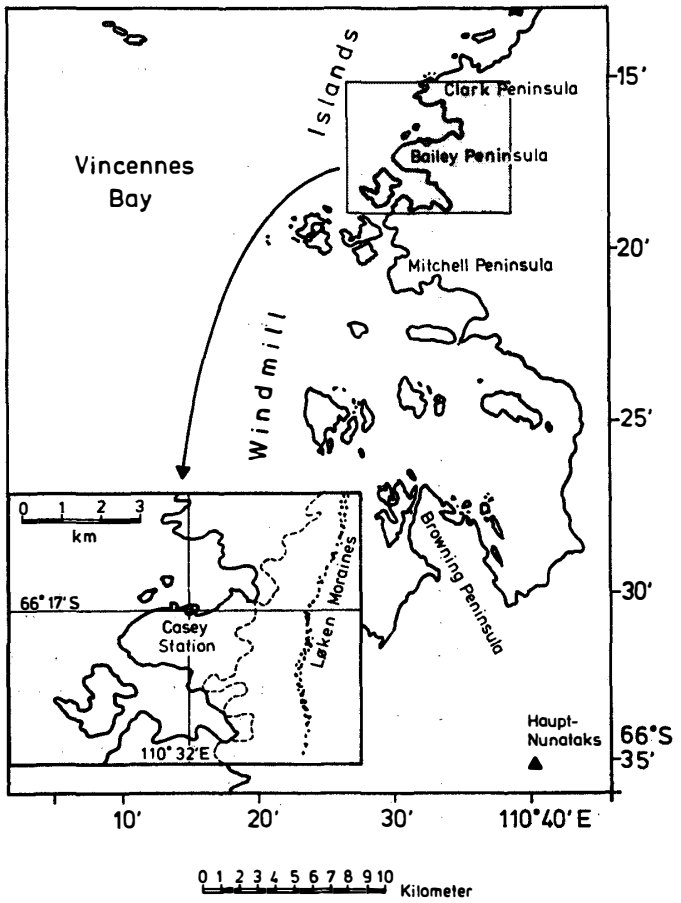

Fig. 1. Map of the location of Casey Station, Wilkes Land.

area covered about 50 × 50 m. Samples were taken from different soil types and covers. As such, 6 depth profiles (each profile comprising intervals of 0–2 cm, 2–4 cm, 4–7 cm), 8 surface samples and one profile in a moss stand were analyzed (Table 1). About 100–500 g of the different horizons were collected by a cleaned and presterilized plastic spoon with 70% ethanol.

The samples were analyzed for a broad spectrum of physical, chemical, and biological parameters. A brief account of the methods is given in Table 2. Some of these parameters were analyzed directly on the field samples: Gross respiration via gas exchange measurements (KAPPEN *et al.*, 1986), ATP via extraction by hot tris-buffer and luciferin/luciferase reaction (ERNST, 1970), water content via drying at 105°C.

All samples were stored immediately after sampling at −20°C and transported deep frozen to the laboratory in Kiel where all further analyses were carried out according with some modifactions related to the special nature of the samples. For details on determinations of carbohydrates and amino acids as well as on the analysis of the bacterial population and its activity related to glucose, see BÖLTER (1990).

Table 1. Description of samples.

Profile	Sample	Depth (cm)	Description
1	1	0–2	dry moss cushion
	2	2–4	sand
	3	4–6	sand
	4		thalli of *Usnea sphacelata*
2	5	0–2	sand
	6	2–4	sand
	7	4–7	sand
3	8	0–2	sand
	9	2–4	sand
	10	4–6	sand
4	11	0–2	sand
	12	2–4	sand
	13	4–6	sand
5	14	0–2	sand
	15	2–4	sand
	16	4–7	sand
6	17	0–2	sand
	18	2–4	sand
	19	4–7	sand
	20	0–1	sand covered with *Alectoria* sp.
	21	0–1	sand covered with *Umbilicaria* sp.
	22, 25	0–1	sand covered with *Candelariella* sp.
	23	0–1	sand covered with *Buellia* sp.
	24	0–1	moss cushion with *Buellia* sp.
	26	0–1	sand covered with algae
	27	0–1	dry moss cushion
7	28	0–2	*Grimmia antarctica*
	29	2–4	moss
	30	4–7	moss, almost turf
	31	0–1	mat of *Nostoc* sp.

Enzymatic activity was analyzed by a modified method of HOPPE (1983) using methylumbelliferyl-labelled substrates which gives an indications of hydrolase activities. Further details than given in Table 2 as well as original data are published for surface samples (BÖLTER, 1989). Table 3 presents the list of all parameters used. In total, the data set used for this study comprises 87 parameters of which some are ratios between originally measured parameters or their derivates.

Table 2. Brief account of analytical methods and references.

Parameter	Method	Reference
Water content	drying at 105°C	
Total organic matter	combustion at 550°C	
Inorganic nutrients/anions and kations	MERCK "Spectroquant" reagent kits	
Particulate organic carbon and nitrogen	HERAEUS CHN-analyzer	
Protein	SIGMA reagent kit	
Carbohydrates	class reaction	DAWSON and LIEBEZEIT (1983)
Free amino acids	ortho-phthalaldehyde reaction	DAWSON and LIEBEZEIT (1983)
Metals	atomic absorption analysis	ORREN *et al.* (1980)
ATP	tris-buffer extraction/ photoluminescence	ERNST (1970)
Bacterial number and biomass	epifluorescence microscopy	ZIMMERMANN *et al.* (1978)
Glucose uptake and respiration	non-kinetic approach	HARRISON *et al.* (1971), MEYER-REIL (1978)
Exoenzymatic activity	methylumbelliferyl-(MUF)-substrates	HOPPE (1983)
Gross respiration	CO_2-gas exchange	KAPPEN *et al.* (1986)

Table 3. Groups of parameters established from the complete linkage clustering of the correlation matrix at $P<0.05$. Parameters labelled with stars (*) or huts (^) refer to subgroups which can be established at a significance level of $P<0.01$.

Group 1:	Nitrate*, sum of inorganic N*, percent of ammonia* and nitrate* of total inorganic N, ratio of inorganic N/P*, protein/proteid ammonia*
Group 2:	Monocarbohydrates*, actual uptake of glucose at 5°C*, 15°C*, 25°C*, bacterial biomass production at 5*, 15*, 25°C*, remineralization rate of glucose at 5*, 15*, and 25°C*
Group 3:	Water content^, loss on ignition^, nitrite^, protein*, particulate organic N* and C*, ratio C/N*, free amino acids*, ATP*, particulate carbohydrates^, ratio particulate carbohydrates/monocarbohydrates*, free amino acids/monocarbohydrates*, reaction on MUF-glucoside at 2°C*, MUF-butyrate at 2* and 18°C*, MUF-phosphate at 2* and 18°C*, MUF-galactoside at 18°C*, MUF-acetate at 2* and 18°C*, turnovertime of glucose at 5, 15 and 25°C.
Group 4:	Ratio bacterial number/biomass*, percentages of cocci $<0.5\,\mu$m of biomass* and number*, rods 1–1.5 μm of biomass* and number*
Group 5:	Proteid ammonia, percentage of cocci 0.5–1 μm of biomass and number
Group 6:	Total bacterial number and biomass, respiration of glucose at 25°C
Group 7:	Percentage of rods 0.5–1 μm of biomass, rods 1.5–2.5 μm of biomass and number
Group 8:	Soluble and total phosphate, iron
Group 9:	Ammonia*, ratio of ammonia/proteid ammonia, reaction on MUF-galactoside at 2°C
Group 10:	Desintegrated phosphate, polyphosphate, ratio polyphosphate/total phosphate
Group 11:	Gross respiration at all incubation temperatures (2, 6, 10, 15, 20, 25°C)

The statistical and mathematical analysis was carried out according to BÖLTER *et al.* (1980) with modifications given by BÖLTER and MEYER (1986). In brief, the original data matrix is treated by a "SPEARMAN" rank-correlation. The resulting correlation matrix is analyzed by different hierarchical cluster algorithms (complete linkage, average linkage and single linkage) in order to differentiate groups of parameters groups of samples after matrix transposition and data normalization. Correlation coefficients are recalculated with regard to the significance levels. The cluster analysis of relationships between parameters is carried out by using absolute correlation coefficients. The cluster analysis of samples is performed with regard to the sign of the correlation coefficient thus giving information about similarity and dissimilarity between samples.

3. Results

3.1. Statistical description of the data set

Individual parameters are characterized by a strong variability. Only 10 of them show a coefficient of variation less than 50%. These parameters are: percent of cocci ($<0.5\,\mu$m and 0.5–1.0 μm) of total bacterial biomass; percent of cocci ($<0.5\,\mu$m) and rods (0.5–1.0 μm) of total bacterial number; pH(H_2O); pH($CaCl_2$); respiration (%) of ^{14}C-glucose at 5, 15 and 25°C.

This great variability of most of the parameters indicates a strong heterogeneity of the system and refers to a great asymmetry of the sampling points represented by their different properties. In spite of this heterogeneity there are a lot of significant correlations between the individual parameters: 45.5% of the correlation matrix is filled with significant correlations ($P<0.05$). However, many of these correlations may be arbitrary. Since it is impossible to consider all interrelationships in detail here, we shall refer to the results of the cluster analysis and the groups identified by this method. They can be regarded as overall parameters of the interactions and describe interrelationships within the parameters and the groups of samples.

3.2. Cluster analysis of parameters

Eleven groups of parameters can be established ($P<0.05$) by using complete linkage clustering (groups must have at least 3 members, Table 3). The largest group, Group 3, combines most of the parameters describing enzymatic activities and turnover times of glucose, *i.e.* potential activities of microbes. Group 3 also contains most of the important soil properties which include water content, loss on ignition, C/N ratio and others. Apart from these parameters are those of the description of the bacterial population as well as those of the actual metabolic rates of glucose, and they are combined in Group 2. Except nitrite, no inorganic constituent is a member of Group 3; such constituents are members of Group 1. It seems evident that there is no segregation of those rates obtained at different temperatures, a fact which was also relevant for the activity parameters in Group 3.

The clustering procedure based on average linkage combines most of the groups obtained by the complete linkage method into a few, very large clusters. As such, the largest cluster contains 41 parameters at $P<0.01$. Except for Groups 4, 7, 8, 10 (Table 3), which remain separated, all other groups are combined to form a large cluster.

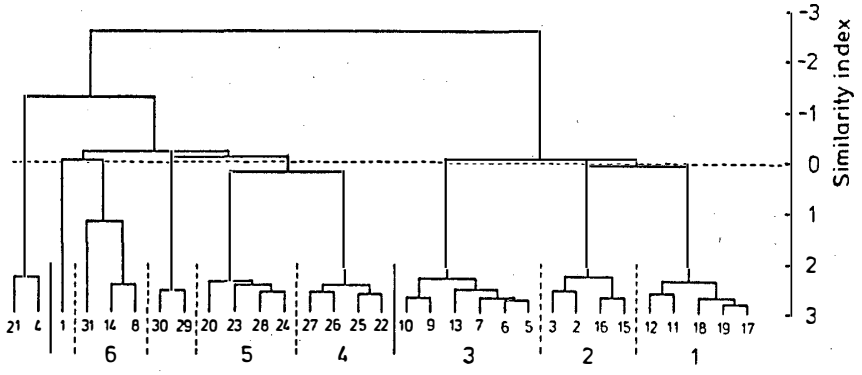

Fig. 2. Dengrogram of the samples (1–31) obtained by complete linkage clustering. The dashed vertical lines indicate separations of groups, the full lines indicate a separation due to the change of the correlation coefficient. The scale of the ordinate (−3 to 3) refers to the correlation coefficient ($P<0.05$: $r=r+1$; $P<0.01$: $r=r+2$; where r=absolute value of the correlation coefficient), for details see text.

3.3. Analysis of samples

The transpositioned and normalized data matrix is analyzed in the same way. However, during this procedure, the sign of the correlation coefficient was used in order to classify the samples with regard to its statistical significance. Figure 2 shows the dendrogram of this cluster analysis. Six groups can be established and these will be considered in more detail.

Members of Groups 1, 2 and 3 cannot be linked by any significant correlation coefficients. These three groups are composed of samples from sandy soils and can be separated significantly from Groups 4, 5 and 6. Group 4 combines samples from soil surfaces. Group 5 again combines surface samples which are covered by *Alectoria* sp. (sample no. 20), *Buellia* sp. (23), a dry moss cushion (24) and a moss surface *Grimmia antarctica* (28). Group 6 combines two surface samples from sandy soils (8, 14) and a surface covered by *Nostoc* sp. Samples 29 and 30 represent the deep layers of a moss stand, samples 4 and 21 are two lichens (*Usnea sphacelata* and *Umbilicaria decussata*, respectively); these four samples remained unclustered during this analysis.

3.4. Statistical description of the groups of samples

The information of the groups of the samples brings us back to the original data set which is splitted into the above-mentioned six groups of samples. The statistical analysis of the parameters is carried out again in order to evaluate parameters suitable as descriptors of these groups. The variations of all characters are inspected for their mean values, ranges, coefficient of variation (V_k=standard deviation/mean value), absolute mean deviation, and the confidence interval (SACHS, 1984; MEYER, 1984). Table 4 shows the result of this analysis when a threshold for $V_k=0.33$ is used, which is recommended by SACHS (1984) in order to define a rather homogeneous statistical distribution. Those parameters which fulfill this condition are further analyzed for their ranges, confidence intervals and absolute mean deviation.

There are only a few parameters which fulfill the condition of $V_k=0.33$. These are mainly parameters of the bacterial population (number and biomass), the pH-values,

and respiration of ^{14}C-glucose at the different temperatures. It is, however, difficult to describe the groups by meaningful thresholds of individual characters, based on the results presented in Table 4. This coincides with the results presented above when analyzing the clusters of parameters of the total data set.

Table 4. Parameters which can be used to describe the groups of samples (Fig. 2) by a homogeneous distribution of their measurements. Groups which can be separated from each other by non-overlapping confidence intervals are shown in a separate column.

Parameter	Groups						Separated groups
	1	2	3	4	5	6	
Water content	×			×	×		1–4–5
Loss on ignition	×	×	×				1–2; 1–3
Nitrite	×						
Magnesium				×			
Ammonia (%) of total N		×		×	×		
Particulate organic C	×	×					
Particulate organic C/N	×	×	×	×		×	4–(1, 2, 3)
Bacterial boimass/number	×			×	×		1–4
Rods 0.5–1 μm, % of biomass	×		×	×		×	
Rods 1–1.5 μm, % of biomass	×			×	×	×	
Rods 1.5–2 μm, % of biomass	×						
Cocci <0.5 μm, % of number	×	×	×	×			
Cocci 0.5–1 μm, % of number	×						
Rods 0.5–1 μm, % of number	×	×		×		×	
Rods 1–1.5 μm, % of number			×				
Rods 1.5–2.5 μm, % of number	×						
ATP	×	×					
MUF-glucosidase reaction (18°C)			×				
MUF-phosphatase reaction (18°C)				×			
Actual uptake of glucose (5°C)	×			×		×	1–(4, 6); 4–6
Remineralization rate of glucose (5°C)				×			
Actual uptake of glucose (15°C)				×		×	4–6
Remineralization rate of glucose (15°C)				×			
Actual uptake of glucose (25°C)				×		×	4–6
Remineralization rate of glucose (25°C)				×		×	
Bacterial biomass production (25°C)				×	×		4–5
pH (H_2O) and ($CaCl_2$)	×	×	×	×	×	×	
Turnovertime of glucose (5°C)					×		
Turnovertime of glucose (15°C)			×				
Turnovertime of glucoss (25°C)			×	×			3–4
Respiration (%) of glucose (5°C)	×	×	×	×			1–2; 1–3
Respiration (%) of glucose (15°C)	×	×	×	×			1–2; 1–3
Respiration (%) of glucose (25°C)	×	×	×	×	×	×	1–3
Sodium			×				
Copper	×				×		1–5
Iron	×		×	×			
Manganese					×		
Zinc			×		×	×	3–6; 5–6

4. Discussion

4.1. General aspects

The original data of this study showed wide ranges in microbial activity and concentrations of organic matter. Although these patterns of distributions of organic and inorganic matter are results of originally occurring processes and reflect the biotic and abiotic background of the system, the different parameters (*e.g.* concentrations on inorganic nutrients and measurements on bacterial activity) act on different time scales and thus it renders difficulty in establishing flow models.

We have to bear in mind that the cluster analyses are based on the calculated correlation matrices, *i.e.* interrelationships between individual characters, and not on the characters themselves. The measure of "similarity" or "distance" between two characters is the correlation coefficient which is tested (and hence accepted or rejected) at a given threshold (here: $P=0.05$). Because of the relatively large numbers of parameters, some randomness must be expected.

It is difficult to prove all interrelationships as shown by correlation analysis; we have to operate at the level of those clusters that give us some hint of the actual interaction levels between specific variables. These levels will be the base of all further consideration without neglecting some interesting details.

It is difficult to compare the present results with others, as only a few soil ecological studies have been carried out in comparable Antarctic environments (*e.g.* those from Syowa Station, NAKATSUBO and INO, 1987; INO and NAKATSUBO, 1986). Most of the published work from Antarctica focus on the composition of the microbial community in the McMurdo Dry Valleys with its special character of cold deserts (*cf.* BLOCK, 1984). Microbial ecological studies like those carried out at Casey Station were conducted mainly in the maritime Antarctic or on Subantarctic islands (*e.g.*, O'BRIEN *et al.*, 1979; BAILEY and WYNN-WILLIAMS, 1982; WYNN-WILLIAMS, 1984; GROBLER *et al.*, 1987; SMITH, 1988).

4.2. Individual results

Some of these results, as they refer to general aspects of soil microbiology, can be confirmed by this study; *e.g.* the importance of moisture content (*cf.* WYNN-WILLIAMS, 1985a, b), low contents of organic material in sandy soils (SMITH and TEARLE, 1985), relationships between the content of nitrogen, loss on ignition, water content (BAILEY and WYNN-WILLIAMS, 1982). More detailed analyses focusing on individual parameters, *e.g.* bacterial biomass, bacterial size classes or nutrients, have been presented in other reports (BÖLTER, 1989, 1990).

The wide ranges of the individual variables seem to be a typical feature of ecosystem from extreme environments, *e.g.* tundra ecosystems. This is well illustrated by the wide span of temperature during the diel profile. SMITH (1986) and BÖLTER *et al.* (1989) describe fluctuations within one day which may exceed 50°C. This example underlines the strong stress factor and—in extrapolation—may result in the asymmetry and heterogeneity of the biotic and abiotic environments. The importance of stress is further supported by details of nutrient analyses and bacterial properties in Antarctic regions (*e.g.*, BAILEY and WYNN-WILLIAMS, 1982; BOOTH and USHER, 1985; FRENCH and SMITH,

1986) for both spatial and temporal investigations.

It could be shown for surface samples (BÖLTER, 1989) that enzymatic activities (hydrolases and phosphatase) generally show optima $>20°C$. Although this may be unexpected in an environment with low mean temperatures, the extremes of temperatures reported by SMITH (1986) from this area should be taken into consideration. It seems to be of great advantage to be able to make use of high energy inputs, though only for short durations. Favorable conditions—availability of nutrients and water at moderate temperatures—are temporally limited at the upper and lower extremes, which result both in a poorness of available water. As such, the microbial community of these ecosystems seem to be more effectively adapted to wide ranges of temperatures than just to low temperatures near zero. The presence of favorable conditions, even with these extended spans in temperature, are short and integrated values of possible microbial activity over longer periods remain small, which has been demonstrated by environmental parameters for the McMurdo Dry Valleys by FRIEDMANN *et al.* (1987) and the Casey Station area by BÖLTER *et al.* (1989). However, in an environment of fast changing physical conditions they seem to be sufficient to sustain a system which obviously acts at the boundary of life processes. Hence, more attention has to be paied to extreme values of metabolic activity which are of great importance. With regard to the high reactivity, this seems to be important for the microbial community to survive in this harsh environment.

4.3. Cluster analyses

We can either consider groups of parameters or individually measured values. This, however, brings us to a state of vagueness in describing ecological patterns and groups of interacting parameters. HOWARD and HOWARD (1987) conclude that "no individual property can be used as a measure of soil bioactivity" and it is safe to assume that this statement can be extended to other soil properties. This points to the evidence of the multi-functional property of the soil system, which has been shown by earlier reports of NANNIPIERI *et al.* (1978, 1979) and BUNNELL *et al.* (1977) who mentioned this for other soil environments. This has also been reported for other ecosystems (BÖLTER and MEYER, 1983, 1986; BÖLTER, 1987).

The data presented here contain both physicochemical parameters and parameters of microbial activity. The cluster analysis of these parameters (Table 3) resulted in classifications of distinguishable groups. Only one of them is a mixture of both kinds of parameters (concentrations and processes), suggesting that processes are mainly controlled by some environmental parameters and nutrients. This relationship has been suggested previously (*e.g.*, WYNN-WILLIAMS, 1984; DAVIS, 1986; CHRISTIE, 1987). It should, however, be borne in mind, that the parameters of microbial and enzymatic activity describe mainly potential activities rather than those of actual processes.

The cluster analysis of the samples revealed generally a separation into two groups, sand samples and samples covered with plant material, *i.e.* samples with significantly higher contents of organic matter. Although this may meet an expected pattern, it is rather difficult to establish distinct variates for discriminations. Table 4 gives some hint and shows 14 characteristics which can be used as describing parameters of the established groups (Fig. 2). Of these, water content, loss on ignition and C/N seem to be

powerful discriminators. Further, we have to consider several characteristics of microbial activity.

This can be verified in general when using only these 14 characters for another cluster analysis of the samples. The result shows—at the level of significant separations—a rather concomitant pattern to that of Fig. 2: Three clusters remain nearly in the same order and can be separated significantly from the others. Shifts occur with samples 20, 28, 29 and 30 which can be regarded more closely related to samples 4 and 21. This, however, needs further verification and more detailed analysis will be conducted in comparison with ordination techniques (M. BÖLTER and D. D. FRENCH, in prep.).

The results of the cluster analysis as shown in Fig. 2 may be due to the following reasons: a) basic differences in the physical structure of the soils which would impose different niches and quality of the substrate itself, and b) the thereby derived secondary niches due to plant cover and further biological/chemical properties. Both the abiotic and the biotic systems may lead to the existence of asymmetries in patterns (MARGALEF, 1979). Physical factors, *e.g.* light input and diffusion, cryoturbation, wind erosion and water drainage, as well as chemical properties, such as nutrient gradients, and biological features (the lack of any continuous bioturbation by mobile organisms) are important parameters of these niches.

5. Concluding Remarks

The terrestrial system of this area is mainly governed by geomorphology, especially in the small scale. The accumulation of eroded material is due to the physical stability of local niches which may give a certain shelter and stabilize the material at least at that time and it can be used for microbial colonization, biochemical and chemical processes. As wind and corresponding turbulence as well as cryoturbation can be regarded as main external energy inputs (besides solar radiation), they may become main driving forces to the system itself. Concomitantly, MARGALEF (1978) considered that oceanic currents are main input of external energy into the pelagic system.

In conclusion, we have to solve a paradox: The Antarctic microbial system is regarded to be very simple with only a few components of producers and consumers. In contrast, this detailed analysis shows a very scattered system on a very small scale, *i.e.* centimeters. These small patches lead to increased surface areas of the contact zones of quite different small-scale ecosystems, which consequently results in enhanced fluxes of energy, matter and information (FRONTIER, 1987).

This hypothesis of organization of these ecosystems needs further investigation, but may be of great interest for extreme environments. "Studies of spatial organization of ecosystems allow an abridged description only when the pattern is clearly the outcome of relatively simple processes, and is influenced by the persistence of the relicts of a long history" (MARGALEF, 1978). This should be especially true for terrestrial ecosystems in the Antarctic. Although these systems may be useful for rather simple descriptive models, it has to be borne in mind that all figures of measured soil properties are only "snapshots" of an immense range of potential of a real variability.

Acknowledgments

The data were obtained during an expedition to Casey Station 1985/86. My thanks go to my colleagues Prof. L. KAPPEN and Mr. A. KÜHN for their help during the field study, logistics and further discussions on methods and results. I also thank Dr. R. I. LEWIS SMITH and R. HANCOCK for their fellowship and stimulating discussions during the expedition. Dr. H. HENNIG, NRIO, Stellenbosch, analyzed the samples for metals by atomic absorption analysis, and the results on particulate carbon and nitrogen were obtained in the laboratory of Prof. B. SATTELMACHER, Kiel. Prof. C. HOPKINS and Dr. M. MEYER gave friendly cooperation and help in discussing the results. The project was funded by the German Research Council (DFG project Ka 390/6-6).

References

BAILEY, A. D. and WYNN-WILLIAMS, D. D. (1982): Soil microbiological studies at Signy Island, South Orkney Islands. Br. Antarct. Surv. Bull., **51**, 167–191.

BLOCK, W. (1984): Terrestrial microbiology, invertebrates and ecosystems. Antarctic Ecology, ed. by R. M. LAWS. London, Academic Press, 161–236.

BÖLTER, M. (1987): Microbiological, planktonic and chemical characteristic and their validity for separation of water masses in the Bransfield Strait, Antarctica. S. Afr. J. Mar. Sci., **5**, 133–143.

BÖLTER, M. (1989): Microbial activity in soils from Antarctica (Casey Station, Wilkes Land). Proc. NIPR Symp. Polar Biol., **2**, 146–153.

BÖLTER, M. (1990): Microbial ecology of soils from Wilkes Land, Antarctica. I; The bacterial population and its activity in relation to dissolved organic matter. Proc. NIPR Symp. Polar Biol., **3**, 104–119.

BÖLTER, M. and MEYER, M. (1983): The sandy beach area of Kiel Fjord and Kiel Bight (western Baltic Sea)—A structural analysis of a shallow water ecosystem. Sandy Beaches as Ecosystems, ed. by A. MCLACHLAN and T. ERASMUS. The Hague, Junk, 263–270.

BÖLTER, M. and MEYER, M. (1986): Structuring of ecological data sets by methods of correlation and cluster analysis. Ecol. Modell., **32**, 1–13.

BÖLTER, M., MEYER, M. and PROBST, B. (1980): A statistical scheme for structural analysis in marine ecosystems. Ecol. Modell., **9**, 143–151.

BÖLTER, M., KAPPEN, L. and MEYER, M. (1989): The influence of microclimatic conditions on potential photosynthesis of *Usnea sphacelata*—A model. Ecol. Res., **4**(3), (in press).

BOOTH, R. G. and USHER, M. B. (1985): Variation in the physical and chemical environment of a maritime Antarctic moss-turf. Br. Antarct. Surv. Bull., **67**, 25–40.

BROWN, J., MILLER, P. C., TIESZEN, L. and BUNNELL, F. L., ed. (1980): An Arctic Ecosystem. Stroudsburg, Dowden, Hutchinson and Ross (US/IBP Synthesis Series 12), 571 p.

BUNNELL, F. L., MILLER, O. K., FLANAGAN, P. W. and BENOIT, R. E. (1980): The microflora; Composition, biomass, and environmental relations. An Arctic Ecosystem, ed. by J. BROWN *et al.* Stroudsburg, Dowden, Hutchinson and Ross, 255–290 (US/IBP Synthesis Series 12).

CAMERON, R. E., KING, J. and DAVID, C. N. (1970): Microbiology, ecology and microclimatology of soil sites in Dry Valleys of Southern Victoria Land, Antarctica. Antarctic Ecology, ed. by M. W. HOLDGATE. London, Academic Press, 702–716.

CHRISTIE, P. (1987): Nitrogen in two contrasting Antarctic bryophyte communities. J. Ecol., **75**, 73–93.

DAVIS, R. C. (1986): Environmental factors influencing decomposition rates in two Antarctic moss communities. Polar Biol., **5**, 95–103.

DAWSON, R. and LIEBEZEIT, G. (1983): Determination of amino acids and carbohydrates. Methods of Seawater Analysis, ed. by K. GRASSHOFF *et al.* Weinheim, Verlag Chemie, 319–346.

ERNST, W. (1970): ATP als indikator für die Biomasse mariner sedimente. Oecologia, **5**, 56–60.

FRENCH, D. D. and SMITH, V. R. (1986): Bacterial populations in soils of a Subantarctic island. Polar Biol., **6**, 75–82.

FRIEDMANN, E. I., MCKAY, C. P. and NIENOW, J. A. (1987): The cryptoendolithic microbial environment in the Ross Desert of Antarctica; Satellite-transmitted continuous nanoclimate data, 1984 to 1986. Polar Biol., **7**, 273–287.

FRONTIER, S. (1987): Application of fractal theory to ecology. Developments in Numerical Ecology, ed. by P. LEGENDRE and L. LEGENDRE. Berlin, Springer, 335–378 (NATO ASI Series G14).

GROBLER, D. C., TOERIEN, D. F. and SMITH, V. R. (1987): Bacterial activity in soils of a Sub-Antarctic island. Soil Biol. Biochem., **19**, 485–490.

HARRISON, M. J., WRIGHT, R. T. and MORITA, R. Y. (1971): Method for measuring mineralisation in lake sediments. Appl. Microbiol., **21**, 223–229.

HOLDING, A. J., HEAL, O. W., MACLEAN, S. F. and FLANAGAN, P. W. (1974): Soil Organisms and Decomposition in Tundra. Stockholm, Tundra Biome Steering Committee.

HOPPE, H.-G. (1983): Significance of exoenzymatic activities in the ecology of brackish water; Measurements by means of methylumbelliferyl-substrates. Mar. Ecol. Prog. Ser., **11**, 299–308.

HOWARD, P. J. A. and HOWARD, D. M. (1987): Numerical classification of forest soils using biological and biochemical properties. Biol. Fert. Soils, **5**, 61–67.

INO, Y. and NAKATSUBO, T. (1986): Distribution of carbon, nitrogen and phosphorous in a moss community-soil system developed on a cold desert in Antarctica. Ecol. Res., **1**, 59–69.

KAPPEN, L., BÖLTER, M. and KÜHN, A. (1986): Field measurements of net photosynthesis of lichens in the Antarctic. Polar Biol., **5**, 255–258.

MARGALEF, R. (1978): The organization of space. Oikos, **33**, 152–159.

MARGALEF, R. (1979): Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol. Acta, **1**, 493–501.

MEYER, M. (1984): Ökologische Datensätze—Programme für AOS-Rechner und BASIC-Taschencomputer (TI-58/59, PC-1211/1212). Braunschweig, Vieweg.

MEYER-REIL, L.-A. (1978): Uptake of glucose by bacteria in the sediment. Mar. Biol., **44**, 293–298.

NAKATSUBO, T. and INO, Y. (1987): Nitrogen cycling in an Antarctic ecosystem. 2; Estimation of the amount of nitrogen fixation in a moss community on East Ongul Island. Ecol. Res., **2**, 31–40.

NANNIPIERI, P., JOHNSON, R. L. and PAUL, E. A. (1978): Criteria for measurement of microbial growth and activity in soil. Soil Biol. Biochem., **10**, 223–229.

NANNIPIERI, P., PEDRAZINNI, F., ARCARA, P. G. and PIOVANILLI, C. (1979): Changes in amino acids, enzyme activities, and biomasses during soil microbial growth. Soil Sci., **127**, 26–34.

O'BRIEN, R. M. G., ROMANS, J. C. C. and ROBERTSON, L. (1979): Three profiles from Elephant Islands, South Shetland Islands. Br. Antarct. Surv. Bull., **47**, 1–12.

ORREN, M. J., EAGLE, G. A. and HENNING, H. F.-K. O. (1980): Variations in trace metal content of the mussel *Choromytilus meridionalis* (KR.) with season and sex. Mar. Pollut. Bull., **11**, 253–257.

SACHS, L. (1984): Angewandte Statistik. Berlin, Springer.

SMITH, H. G. and TEARLE, P. V. (1985): Aspects of microbial and protozoan abundances in Signy Island fellfields. Br. Antarct. Surv. Bull., **68**, 83–90.

SMITH, R.I.L. (1984): Terrestrial plant biology of the sub-Antarctic and Antarctic. Antarctic Ecology, ed. by R. M. LAWS. London, Academic Press, 61–162.

SMITH, R.I.L. (1985): Nutrient cycling in relation to biological productivity in Antarctic and Sub-Antarctic terrestrial and freshwater ecosystems. Antarctic Nutrient Cycles and Food Webs, ed. by W.R. SIEGFRIED *et al.* Berlin, Springer, 138–155.

SMITH, R.I.L. (1986): Plant ecological studies in the fellfield ecosystem near Casey Station, Australian Antarctic Territory, 1985–86. Br. Antarct. Surv. Bull., **72**, 81–91.

SMITH, V. R. (1988): Production and nutrient dynamics of plant communities on a Sub-Antarctic island. Polar Biol., **8**, 255–269.

WYNN-WILLIAMS, D. D. (1984): Comparative respirometry of peat decomposition on a latitudinal transsect in the maritime Antarctic. Polar Biol., **3**, 173–181.

WYNN-WILLIAMS, D. D. (1985a): The Signy Islands terrestrial sites. XVI; Peat O_2-uptake in a moss turf relative to edaphic and microbial factors. Br. Antarct. Surv. Bull., **68**, 47–59.

WYNN-WILLIAMS, D. D. (1985b): The Signy Islands terrestrial sites. XVII; Peat O_2-uptake in a moss carpet relative to edaphic and microbial factors. Br. Antarct. Surv. Bull., **68**, 61–69.

ZIMMERMANN, R., BECKER-BIRCK, J. and ITURRIAGA, R. (1978): Simultaneous determination of the total number of aquatic bacteria and the number thereof involved in respiration. Appl. Environ. Microbiol., **36**, 926–935.

(Received January 9, 1989; Revised manuscript received August 14, 1989)