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Microbiological Communities and Properties of Arctic Soils: Results of the Tundra Northwest Expedition 1999 (Nunavut and Northwest Territories, Canada)

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Abstract: Microbial communities were analyzed at 17 sites visited during the expedition Tundra Northwest 1999 (TNW-99) by microscopic analyses (epifluorescence microscopy and image analyses). The data were used to describe the communities of bacteria, fungi and algae in detail by number, biovolume and biomass. Great variability was found, which could be related to organic matter content of soils and features of vegetation patterns. The amounts (numbers and abundance) of organisms and data on microbial biomass are discussed in relation to other polar environments of the Northern and Southern Hemispheres.

Zusammenfassung: Mikrobielle Gemeinschaften von 17 arktischen Boden-Standorten, beprobt während der Expedition "Tundra Northwest 1999", wurden mittels Epifluoreszenz-Mikroskopie und Bildauswertung untersucht. Dabei wurden Gemeinschaften von Bakterien, Pilzen und Algen hinsichtlich Zahl und Biovolumen und Biomasse bestimmt. In den Böden wurde eine große mikrobiologische Variabilität gefunden, die mit der Menge an organischem Material sowie der Vegetationsdecke korrelierte. Die gefundenen Daten werden mit Ergebnissen anderer Untersuchungen aus den Polargebieten der nördlichen und südlichen Hemisphären verglichen und diskutiert.

INTRODUCTION

Soil micro-organisms bacteria, fungi and algae represent the driving forces for the turnover of soil organic matter. They control organic matter accumulation and mineralization, releasing CO_2 and CH_4. Although the polar environmental conditions would seem to be unfavourable for life, the abundance of micro-organisms, their high potential for activity and metabolic response to changes in living conditions make them important indicators of the effects of global change. Extensive areas of the arctic landscape are known to be in transition already. In response, micro-organisms will have changed their communities and physiological properties before such changes might be monitored by new plant associations, or animal invasions. Indeed, records on these organisms can give us information about ongoing processes in soil biology.

The general role of micro-organisms in soil processes is well known. But studies on their abundance and activity in the extreme north have been performed only locally. Some important results have been reported, although they refer mostly to colony-forming micro-organisms (e.g., BOYD & BOYD 1971, PARINKINA 1974, 1992, COCKELL et al. 2001). Other studies in these regions on plants or soils generally have neglected micro-organisms or given them only slight attention (BLISS 1997). Results from the Russian tundra showing the role of micro-organisms in arctic soils have been published recently by BÖLTER & KANDA (1997), SCHMIDT (1999), and SCHMIDT & BÖLTER (2002).

The expedition TNW-99 was dedicated to the search for aspects of life in the Canadian Arctic at different scales (ERIKSEN et al. 2006). Preliminary results have been published in the cruise report (BÖLTER 1999, GRÖNLUND 1999), as well as data on soil algae (BÖLTER 2001) and soil (BÖLTER et al. 2006). The working group for small-scale processes thus put its focus on the life of microbial organisms, i.e., bacteria and fungi. Our aim was to provide data on sub-surface biomass in correlation with the main focus of other working groups, namely, various higher plants (ERIKSEN et al. 2006, LARSSON & LEVESQUE 2002). The data set provided here is, then, another piece of the puzzle of life in arctic soil (HENRY et al. oral com.).

MATERIAL AND METHODS

Site Descriptions and Sampling

Sites in Canada (Fig. 1) were visited during the expedition TNW-99 from July 2 to August 30. Site locations and their specific local descriptions are given in Tables 1a and 1b. Detailed descriptions of them by vegetation patterns as well as photos of the sites and from some soils pits are being presented by ERIKSON et al. (2006), data on soils by BÖLTER et al. (2006). During Leg 1 of TNW-99 (sites 1-9), sampling was carried out by the author; on the Leg 2 (sites 10-17) it was done by Dr. Anders Dahlberg, however, only for surface horizons. Samples were taken at dry and mesic locations according to the soil horizons; a surface layer (0-2 cm) sample was collected separately in each case. Further, several other sites were sampled only at the surface in order to demonstrate local variability.

Analytical Methods

Samples taken during Leg 1 were examined onboard the ship at low microscopic magnification for detritus material and soil animals, e.g., nematodes, collembolans. Samples were stored deep-frozen before analyses for micro-organisms, which were performed in the laboratory in Kiel by epifluorescence microscopy. Acridine orange staining and image analysis *(Leica Quantimet 500*™) were methods used. Analysis of the microbiological organisms included counts and biovolume determinations using polycarbonate membranes with pore size 0.2 μm for bacteria and 3.0 μm for algae. Bacteria were measured for

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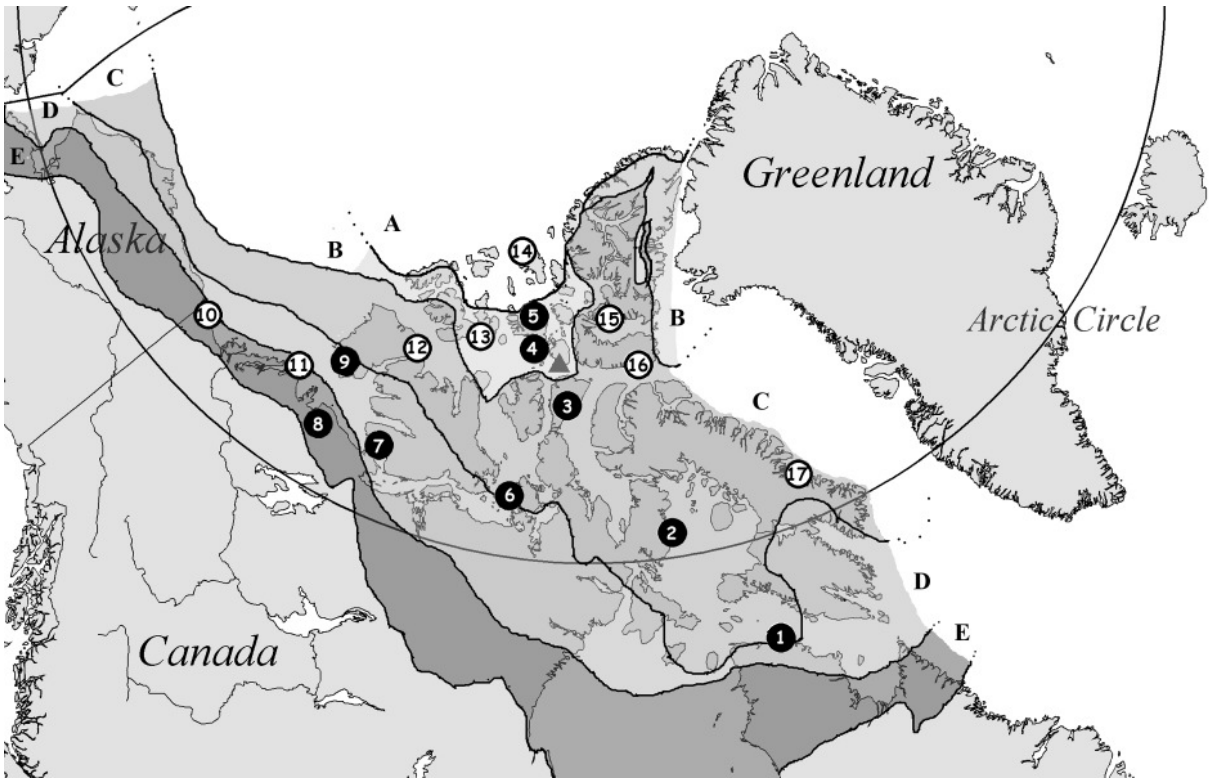

Fig. 1: Sampling sites in the Canadian Arctic visited during the "Tundra Northwest 1999" expedition. Circles numbered 1 through 9 = sites visited during Leg 1; circles, numbered 10 through 17 = sites visited during Leg 2. Solid-drawn lines = borders between the five bioclimatic zones proposed by ELVEBAKK et al. (1999). A = arctic polar desert, B = northern arctic tundra, C = middle arctic tundra, D = southern arctic tundra, and E = arctic shrub-tundra.

Abb. 1: Beprobungsorte während der Expedition "Tundra Northwest 1999". Die Stationen 1-9 (Kreise) waren Teil des ersten Fahrtabschnittes, die Stationen 10-17 lagen im zweiten Fahrtabschnitt. Die Einteilung der bioklimatischen Zonen erfolgte nach ELVEBAKK et al. (1999) in A = arktische Polarwüste, B = nördliche arktische Tundra, C = mittlere arktische Tundra, D = südliche arktische Tundra, E = arktische Strauchtundra.

Location	Date	Latitude	Longitude	Moisture	Code	Depth (cm)	Samples*
Nuuk	25.06.99	65°10.8'	51° 44.68'	Mesic	N	0-3	N1-N3
Ungava	02.07.99	62°22.25	73° 47.76	Mesic	1m*	0-2; 4-8; 20-24;50-54	1ma (0-4 cm)
Melville	05.07.99	67°35.02	81° 42.20	Dry	2d*	0-2; 2-7; 10-20; 60-65	2za-2zg
Peninsula	05.07.99	67°53.11	81 ° 43.02	Mesic	2m	0-5; 5-9; 30-35	
Somerset Island	10.07.99	72°55.38	93° 27.02	Dry	3d	0-2; 10-14; 50-55	3za-3zb
	10.07.99	72°55.31	93° 26.73	Mesic	3m	0-4; 4-7; 35-40	
Resolute	12.07.99	74°41.99'	94° 49.78	Dry	R	0-2	R1-R2
Bathurst Island S	13.07.99	75°04.42	98° 30.98	Dry	4d	0-4; 4-8; 45-50	4za-4zb
	13.07.99	75°04.34	98° 31.01	Mesic	4m	0-4; 4-8; 45-50	
Bathurst Island E	16.07.99	76°26.22	97° 56.64	Mesic	5m	0-4; 4-8	5za-5zd
King William	20.07.99	69°06.66	98° 55.09	Dry	6d	0-2; 2-4; 40-44; 74-78	6za
Island	20.07.99	69°06.06	98° 55.90	Mesic	6m	0-2; 4-8; 10-14; 45-50	
Wollaston	23.07.99	69°26.46	114° 43.50	Dry	7d	0-2; 2-4; 10-14; 85-90	7za-7zb
Peninsula	23.07.99	69°26.40	114° 43.51	Mesic	7m	0-4; 4-8; 30-34; 105-110	
Paulatuk	26.07.99	69°45.84	122° 02.84	Dry	8d	0-3; 4-8; 25-30; 95-100	8za-8zc
	26.07.99	69°45.85	122° 03.02	Mesic	8m	0-4; 4-8; 20-24; 100-105	
Banks Island S	28.07.99	71°43.01	123° 44.14	Dry	9d	0-4; 4-8; 80-85	9za; 9zb
	28.07.99	71°42.96	123° 44.36	Mesic	9m	0-4; 4-8; 30-35; 50-55	

Tab. 1a: Geographical items of the locations sampled during the expedition TNW-99, Leg 1. * surface samples (0-2 cm) taken from sites with local special properties, e.g., plant cover, algae and others.

Tab. 1a: Geographische Daten zu den Probenorten während der Expedition TNW-99, Abschnitt 1. * Oberflächenproben (0-2 cm) von Standorten mit besonderen Eigenschaften, z.B. Vegetation, Algen et al..

Location	Date	Latitude Longitude	Moist.	Code	Depth (cm)
Ivvavik	04.08.99	69°25.10' 139°38.40'	Dry	10m	0-4
	08.08.99	70°29' 127°50'	Dry	10d	0-4
Cape Bathurst	08.08.99	70°29' 127°50'	Mesic	11d	0-10
	10.08.99	73°37.32' 115°52.02'	Dry	11m	0-10
Banks Island North	10.08.99	73°37.33' 115°51.43'	Mesic	12d	0-4
	13.08.99	75°06.35' 107°38.11'	Dry	12m	0-4
Melville Island	13.08.99	75°06.37' 107°38.35'	Mesic	13d	0-4
	18.08.99	78°55.59' 104°38.21'	Dry	13m	0-4
Ellef Ringnes Island	18.08.99	78°55.54' 104°38.34'	Mesic	14d	0-4
	22.08.99	76°31.00' 86°46.08'	Dry	14m	0-4
Ellesmere Island	22.08.99	76°31.07' 86°46.01'	Mesic	15d	0-4
	25.08.99	74°32.49' 82°47.19'	Dry	15m	0-4
Devon Island	25.08.99	74°32.49' 82°47.10'	Mesic	16d	0-4
	30.08.99	68°26.21' 66°49.24'	Dry	16m	0-4
Baffin Island	30.08.99	68°26.22' 66°49.24'	Mesic	17d	0-4
	04.08.99	69°25.10' 139 38.40'	Dry	17m	0-4

Tab. 1b: Geographical items of the locations sampled during the expedition TNW-99, Leg 2.

Tab. 1b: Geographische Angaben zu den Probenorten während der Expedion TNW-99, Abschnitt 2.

length and regarded as cocci when smaller than 0.25 μm, as rods when larger than 0.25 μm. Width was estimated according to an approximation devised by BÖLTER et al. (1993); geometrical formulas were used to calculate biovolume and surface for bacteria and algae depending on their size and shape.

For some analyses of groups of sampling sites, the following subsets of samples were used: a) samples 0-4 cm; b) samples 0-10 cm; c) samples 0-4 cm dry sites; d) samples 0-4 cm mesic sites; e) samples >10 cm; f) samples >10 cm dry sites; g) samples >10 cm mesic sites. Only simple descriptive statistical entities (means, medians, minima, maxima) were applied as normal distributions of the data sets could not be assumed.

RESULTS

First microscopic inspections on board the ship directly after return from the sampling provided a preliminary description of the metazoan community (Tab. 2). Most soils contained nematodes and collembolans. Some surface layers, especially those from moist areas, also showed a few rotifers and even copepods. Nematodes and collembolans were not restricted to the topmost layers but were elevated in number generally in the upper ten centimetres beneath covers of moss cushions or

Site* / Sample	Depth	Faeces	Metazoans*	Fungi
N	0-3			many fungi
N	0-3			some fungi
N	0-3		nem*	some fungi
1m	0-4	caribou,	nem, col	many fungi
1ma	0-2	fox, lemming		some fungi
2d	0-2	caribou,	nem	many fungi
2m	0-5	caribou.	nem, col, rot	many fungi
2za	0-2		nem	few fungi
2zb	0-2		nem	
2zc	0-2		nem, rot	
2zd	0-2			
2ze	0-2		nem, rot	some fungi
2zf	0-2		nem	
2zg	0-2		nem	
3d	0-2	musk ox	nem, col	
3m	0-4	musk ox	nem, col	many fungi
3za	0-2			
3zb	0-2		nem	
R	0-2			
4d	0-4			
4m	0-4		nem, col, cop	
4za	0-2			
4zb	0-2			
5m	0-4		nem, col	
5za	0-2		nem	
5zb	0-2			
5zc	0-2			
5zd	0-2		nem	
6d	0-2			
6m	0-2		col	
6za	0-2		nem, cop	
7d	0-2	musk ox	nem	
7m	0-4	Car.,musk	nem, col, rot	
7za	0-2			
7zb	0-2			many fungi
8d	0-3		nem, rot	
8m	0-4	grizzly	nem, col	
8za	0-2		nem, olig	
8zb	0-2			
8zc	0-2		nem	
9d	0-4	musk ox	n.d.	
9m	0-4	musk ox	col	
9za	0-2			
9zb	0-2			
10d	0-4	caribou,	col	
10m	0-4	musk ox,		
11d	0-10	caribou.		
11m	0-10	musk ox,		
12m	0-4	musk ox,		
13d	0-4	hare, carib..	col	
13m	0-4	musk ox,		
14d	0-4	caribou.	col	
14m	0-4	geese		
15d	0-4	hare, musk ox,	col	
15m	0-4	geese,		
16m	0-4	musk ox,		
17m	0-4	geese,		

Tab. 2: Results of onboard microscopic inspections of surface samples (cf. Tab. 1). N = reference sample from Nuuk; R = reference samples from Resolute; nem = Nematodes, col = Collembolans, cop = Copepod, rot = Rotifers, olig = Oligochaeta.

Tab. 2: Ergebnisse der ersten mikroskopischen Untersuchungen der Bodenproben (s. Tab. 1). N = Referenzprobe in Nuuk, R = Referenzproben von Resolute; nem = Nematoden, col = Collembolen, cop = Copedoden, rot = Rotifera, olig = Oligochaeta.

moss-and-lichen crusts. Further, several samples contained an abundance of fungi, probably basidiomycetes from their size and hook-like cell connections.

Results from the epifluorescence microscopy for bacterial communities in soil profiles of dry and mesic sites are given in Table 3. It is evident that the surface layers, partly also the layers just beneath them, held the most bacteria and greatest biomass. Sites 3m, 5m, 6d, 6m showed extreme values, higher than 10^9 cells g^{-1}. These figures were directly related to the amount of organic matter, which at these places exceeded the mean by far (BÖLTER et al. 2006); probably, this variability is an effect of local variation in soil properties.

Such local variability becomes even more evident when focusing on the surface layers (Tab. 4). Mesic sites had the highest numbers of organisms and of those with large cells, and the greatest biovolume. This finding was related to a shift in the community from small rods (0.5-1.0 µm) to bigger rods and a smaller proportion of the smallest sized cocci (0.2-0.5 μm). The latter class of cocci made up to 55 % in some soils and thus determined the biovolume distribution (Tab. 5). The surface samples did not reveal that big a difference in shares of rods and cocci, as the MCV relies only partly on the different environmental conditions of the dry from the mesic sites.

Soil samples from deep horizons showed a community of significantly smaller size, based on both the overall descriptors (TBN and BBM) and the individual ones (MCV and MBS). A different situation was documented for the deep layer horizons at the mesic sites. Table 5 shows the summarized data of the shifts in size classes and their contributions to the total bacterial community. It was not possible to differentiate all individual groups by the data sets. Significant discrimination was only possible for all surface samples (depths 0-10 cm) and all deep layer samples (depth >10 cm). However, it was not possible to split dry and mesic sites by these parameters.

Small cocci contribute only a low percentage to the total number, and even less to the total volume and surface of the bacterial community. High percentages of cocci could normally be found in deep layers or in samples from dry surfaces, though some exceptions existed – and were responsible for the distribution patterns in the sample groups (Tab. 5). Nearly 70 % of all samples have less than 20 % of these cocci cells, another 20 % of samples show a cocci share between 20 and 30 %. The most abundant group of bacterial cells were small rods (0.25-0.75 μm); 83 % of all the samples had more of these bacterial cells (70-80 %) than any other type. This high number has the most responsibility for the generally uniform pattern of the overall community. These cells also contribute most to total cell volume and total cell surface (Tab. 5). Large cells (lengths >1.5 μm, >1.75 μm) are seldom seen and contribute generally less than 1 % (mean value) of all cells numbers. Their presence, however, indicates high organic matter content – they thus occur mostly in surface samples of mesic sites.

The statistical analyses show that separations for individual sample groups can be performed. This holds true for the share of cocci in their contributions to TBN, BBV and TBS. Hence, a similar pattern can be shown, as above, for the overall descriptors, i.e., the distribution of cocci can be regarded as

Site No.	horizon depth (cm)	TBN n* 10^9 g^{-1} d.wt.	BBV n* 10^9 µm^3 g^{-1}	MBCV µm^3	MBS µm^2	TBS cm^2	MBCV / MBS µm
1m	0-4	0.764	34.6	0.045	0.56	4.28	0.081
1m	4-8	0.675	20.5	0.03	0.45	3.01	0.068
1m	20-24	0.057	0.71	0.013	0.23	0.13	0.054
1m	50-54	0.054	0.67	0.013	0.23	0.12	0.054
2d	0-2	0.299	8.74	0.029	0.44	1.32	0.066
2d	2-7	0.342	12.7	0.037	0.59	1.82	0.070
2d	10-20	0.119	3.22	0.027	0.42	0.5	0.065
2d	60-65	0.077	1.42	0.019	0.32	0.24	0.058
2m	0-5	0.316	5.55	0.018	0.3	0.95	0.058
2m	5-9	0.059	1.2	0.02	0.34	0.2	0.059
2m	30-35	0.130	2.94	0.023	0.37	0.48	0.061
3d	0-2	0.656	18	0.027	0.43	2.84	0.063
3d	10-14	0.149	5.15	0.034	0.51	0.76	0.068
3d	50-55	0.118	3.13	0.027	0.42	0.5	0.063
3m	0-4	2.494	107	0.043	0.59	14.66	0.073
3m	4-7	0.471	16.8	0.036	0.51	2.41	0.070
3m	35-40	0.271	8.84	0.033	0.48	1.31	0.067
4d	0-4	0.377	14.8	0.039	0.55	2.08	0.071
4d	4-8	0.263	9.45	0.036	0.52	1.38	0.069
4d	45-50	0.079	2.15	0.027	0.42	0.33	0.064
4m	0-4	0.161	4.98	0.031	0.46	0.75	0.067
4m	4-8	0.188	9.01	0.048	0.64	1.2	0.075
4m	45-50	0.146	4.82	0.033	0.43	0.71	0.068
5m	0-4	1.069	31.1	0.031	0.47	5.03	0.066
5m	4-8	0.186	4.37	0.023	0.38	0.7	0.062
6d	0-2	1.665	62.6	0.038	0.54	8.97	0.070
6d	2-4	0.058	0.99	0.017	0.3	0.17	0.058
6d	40-44	0.023	0.8	0.035	0.49	0.11	0.070
6d	74-78	0.005	0.19	0.038	0.51	0.03	0.074
6m	0-2	1.215	54.4	0.045	0.62	7.5	0.072
6m	4-8	1.675	58.8	0.035	0.51	8.63	0.068
6m	10-14	0.031	0.86	0.028	0.43	0.13	0.065
6m	45-50	0.043	1.26	0.029	0.45	0.19	0.065
7d	0-2	0.514	17.9	0.035	0.51	2.64	0.068
7d	2-4	0.158	6.02	0.038	0.55	0.87	0.069
7d	10-14	0.165	4.9	0.03	0.45	0.75	0.066
7d	85-90	0.115	2.71	0.024	0.38	0.44	0.062
7m	0-4	0.463	16.6	0.036	0.52	2.42	0.068
7m	4-8	0.106	2.31	0.022	0.35	0.37	0.062
7m	30-34	0.114	4	0.035	0.51	0.58	0.069
7m	105-110	0.020	0.57	0.028	0.43	0.09	0.065
8d	0-3	0.184	7.77	0.042	0.59	1.08	0.072
8d	4-8	0.145	5.72	0.04	0.57	0.82	0.070
8d	25-30	0.095	2.07	0.022	0.35	0.34	0.062
8d	95-100	0.023	0.41	0.017	0.29	0.07	0.059
8m	0-4	0.268	11.6	0.043	0.6	1.59	0.073
8m	4-8	0.196	8.07	0.041	0.58	1.14	0.071
8m	20-24	0.166	1.67	0.01	0.2	0.33	0.050
8m	100-105	0.012	0.131	0.011	0.22	0.03	0.050
9d	0-4	0.174	5.7	0.033	0.49	0.86	0.067
9d	4-8	0.077	1.87	0.024	0.39	0.3	0.062
9d	80-85	0.032	0.63	0.02	0.34	0.11	0.058
9m	0-4	0.370	14.2	0.038	0.54	2.01	0.071
9m	4-8	0.354	13.6	0.038	0.54	1.92	0.071
9m	30-35	0.201	8.87	0.044	0.62	1.24	0.072
9m	50-55	0.178	6.26	0.035	0.52	0.93	0.068

Tab. 3: Data on the bacterial communities of soil profiles. TBN = total bacteria number; BBV = total bacterial biovolume; MBCV = mean bacterial cell volume; MBS = mean bacterial surface; TBS = total bacterial surface.

Tab. 3: Daten zu den Bakteriengemeinschaften in den Bodenprofilen. TBN: Gesamtzahl, BBV = gesamtes Bakterienbiovolumen, MBCV = mittleres Bakterienvolumen, MBS = mittlere Bakterienoberfläche, TBS = gesamte Bakterienoberfläche.

sampl.	n	TBN				BBV				MCV				MBS			
		mean	med	x_{min}	x_{max}	mean	med	x_{min}	x_{max}	mean	med	x_{min}	x_{max}	mean	med	x_{min}	x_{max}
all	98	0.35	0.20	0.01	2.49	12.80	7.30	0.13	107.0	0.033	0.033	0.010	0.077	0.48	0.49	0.20	0.89
0-2	58	0.46	0.34	0.04	2.49	17.50	11.10	0.87	107.0	0.035	0.034	0.012	0.077	0.57	0.50	0.22	0.89
0-10	30	0.51	0.31	0.06	2.49	18.97	10.53	0.99	107.0	0.034	0.036	0.017	0.048	0.50	0.52	0.3	0.64
0-2 d	31	0.38	0.30	0.06	1.67	13.49	9.40	0.87	62.6	0.033	0.033	0.012	0.077	0.49	0.49	0.22	0.89
0-2 m	24	0.58	0.42	0.04	2.49	23.07	15.45	1.06	107.0	0.037	0.036	0.018	0.052	0.53	0.52	0.30	0.70
>10	25	0.10	0.10	0.01	0.27	2.74	2.07	0.13	8.87	0.026	0.027	0.010	0.044	0.40	0.42	0.20	0.62
>10 d	12	0.08	0.09	0.01	0.17	2.23	2.11	0.19	5.15	0.027	0.027	0.017	0.038	0.41	0.42	0.29	0.51
>10 m	13	0.11	0.11	0.01	0.27	3.20	1.67	0.13	8.87	0.026	0.028	0.010	0.044	0.39	0.43	0.20	0.62

Tab. 4: Statistical data for bacterial communities in different soil groups. all = all samples; 0-2 = all surface horizons (0-2 and 0-4 cm); 0-10 = all samples from horizons 0-10 cm; 0-2 d (m) = all samples 0-2 and 0-4 cm from dry (d) and mesic (m) sites; >10 = all samples from depth >10 cm; >10d (m) = all samples from depths >10 cm from dry (d) and mesic (m) sites; n = number of samples per group; TBN = total bacterial number (n x 10^9 g^{-1}); BBV = total bio volume bacterial (10^6 μm^3 g^{-1} d.wt.); MCV = mean cell volume (μm^3); MBS = mean bacterial surface (μm^2); mean = arithmetic mean value; med = median value; x_{min} = minimum value; x_{max} = maximum value.

Tab. 4: Statistische Angaben zu den Bakteriengemeinschaften in verschiedenen Gruppen der Bodenproben. All = alle Proben. 0-2 = alle Oberflächenhorizonte (0-2 und 0-4 cm). 0-10 = alle Probenhorizonte 0-10 cm. 0-2d(m) = alle Proben (0-2 cm und 0-4 cm) von trockenen (d) bzw. mesischen (m) Standorten. >10 = alle Proben der Tiefen >10 cm. >10d (m) = alle Proben >10 cm von trockenen (d) bzw. mesischen (m) Standorten; n = Probenanzahl, TBN Gesamtzellzahl (n x 10^9 g^{-1} d.wt.), BBV = Gesamtbiovolumen (10^6 μm^3 g^{-1} d.wt.), MCV = mittleres Zellvolumen (μm^3), MBS = mittlere Zelloberfläche (μm^2), mean = arithmetisches Mittel, med = Medianwert. x_{min} = Minimalwert, x_{max} = Maximalwert.

	Cocci (%) of			Rods (%)		
	n	Vol.	Surf.	0.25-0.75	0.76-1.25	>1.25
All samples (n = 96)						
x_{min}	6.5	0.3	0.7	44.3	0.0	0.0
x_{max}	55.7	12.6	37.3	82.2	26.6	17.4
mean	18.7	2.3	4.8	68.8	10.6	1.8
median	14.8	1.4	3.0	69.3	9.5	1.3
Surfaces 0-4 cm (n = 56)						
x_{min}	6.5	0.3	0.7	50.0	1.1	0.0
x_{max}	48.1	9.0	37.3	81.8	26.6	17.4
mean	16.0	1.6	3.9	69.3	12.5	2.2
median	14.0	1.2	2.6	69.9	11.7	1.6
Samples 0-10 cm (n = 30)						
x_{min}	9.6	0.6	1.4	57.7	2.4	0.0
x_{max}	39.8	7.5	13.3	78.6	21.7	7.5
mean	18.0	2.0	4.1	67.8	12.3	1.9
median	14.3	1.2	2.5	67.9	13.0	1.5
Surfaces 0-4 cm, dry (n = 30)						
x_{min}	6.5	0.3	0.7	50.0	1.1	0.0
x_{max}	48.1	9.0	16.6	81.8	26.6	17.4
mean	15.8	1.7	3.5	70.7	11.5	2.0
median	13.0	1.2	2.5	71.8	10.4	1.3
Surfaces 0-4 cm, mesic (n = 23)						
x_{min}	6.7	0.4	0.9	57.7	2.4	0.0
x_{max}	39.8	7.1	37.3	78.7	26.1	6.3
mean	16.5	1.6	4.8	68.2	13.2	2.1
median	14.8	1.4	2.8	67.7	12.4	1.9
Samples >10 cm (n = 25)						
x_{min}	8.1	0.6	1.4	44.3	0.0	0.0
x_{max}	55.7	12.6	21.6	82.2	19.8	7.2
mean	24.5	3.7	6.9	68.3	6.1	1.1
median	20.8	2.1	4.5	70.6	5.3	0.5
Samples >10 cm, dry (n = 12)						
x_{min}	10.2	1.1	2.2	54.2	0.0	0.0
x_{max}	44.1	6.3	12.1	82.2	12.9	7.2
mean	22.6	2.9	5.6	71.1	4.9	1.3
median	22.0	2.3	4.6	71.0	4.6	0.3
Samples >10 cm, mesic (n = 13)						
x_{min}	8.1	0.6	1.4	44.3	0.0	0.0
x_{max}	55.7	12.6	21.6	78.4	19.8	2.6
mean	26.3	4.5	8.0	65.7	7.2	0.8
median	19.7	1.6	3.6	69.8	8.1	0.6

representative of the bacterial community. The analysis of rods was performed for their percentages in the three size classes 0.25-0.75 μm, 0.75-1.25 μm, and >1.25 μm. The wealth of the smallest rods in all samples results in their lack of usefulness as discriminators for sample groups; data on these organisms apply only to themselves. Similarly, the frequency of rods >1.25 μm is not high enough to used in separating groups of sampling stations. Which leaves the midsized rods (0.75-1.25 μm), and discrimination of the sample groups can be undertaken using them.

Autotrophic micro-organisms

Autotrophic micro-organisms, i.e., soil algae and cyanobacteria, occurred only in surface layers (0-2 cm). Only 27 samples of those 56 samples considered show an occurrence of autotrophs, this number is about 50 % (Tab. 6). The occurrence of algae cannot be related to the actual water content of the soil. The mean water content of samples with algae is 29.6 % (range: 4.9-66.2 %) of those without algae is 17.8 % (range: 4.8-50.3 %). Hence, there is no evidence for a significant differentiation between these sites with regard to their actual water contents.

DISCUSSION

Invertebrates

Grazers, i.e., nematodes, collembolans and rotifers, were found in soils where organic matter had accumulated, being

Tab. 5: Statistical data of the shares (%) of cocci (<0.25 μm) on total bacterial number (n), total bacterial volume (Vol.), total bacterial surface (Surf.) and shares (%) of rod shaped bacteria of three length (μm) size classes for different soil samples.

Tab. 5: Statistische Angaben zu den Anteilen (%) der Kokken (<0.25 μm) an der Gesamtzahl der Bakterien (n), dem Gesamtbiovolumen (Vol.), der Gesamtoberfläche (Surf.) sowie den Anteilen (%) der stäbchenförmigen Bakterien (drei Längenklassen in μm) für verschiedene Probengruppen.

Sample	TAN ($n\ 10^6\ g^{-1}$ d.wt.)	ABV ($10^6\ \mu m^3\ g^{-1}$ d.wt.)	% BBV of (BBV+ABV)
4	1.527	112.0	23.6
18	0.406	27.10	25.8
19	0.592	171.0	6.8
20	0.277	20.2	32.6
21	1.043	53.3	49.3
22	0.542	114.0	3.0
24	0.407	42.3	6.0
28	0.824	44.9	70.4
45	0.209	17.0	64.7
48	1.307	187.0	9.6
49	0.447	348.0	5.7
51	0.802	69.3	28.3
52	1.577	171.0	26.8
56	0.543	141.0	27.8
61	0.308	94.0	1.1
66	1.473	322.0	4.9
72	0.402	112.0	10.4
77	0.338	12.80	47.5
82	0.665	156.0	2.7
83	0.804	350.0	3.6
84	0.776	347.0	2.1
99	2.378	1310.0	1.6
102	1.333	576.6	7.2
104	0.482	526.1	2.0
105	0.658	513.1	3.1
111	0.620	238.0	2.5
114	1.119	343.0	14.6

Tab. 6: Distribution of autotrophs in soil samples and shares of bacteria. TAN = total number of autotrophs; ABV = autotrophic biovolume; BBV = bacterial biovolume.

Tab. 6: Verteilung autotropher Organismen in den Bodenproben und Anteile der Bakterien. TAN = Gesamzahl autotropher Zellen, ABV = Biovolumen autotropher Zellen, BBV = bakterielles Biovolumen.

found close to plant roots or underneath the cover of mosses. Comparable situations are described for soils from the Antarctic Peninsula region (BÖLTER et al. 1997) and Antarctic deserts (e.g., FRECKMANN & VIRGINIA 1998). These organisms contribute significantly to changes in structure and composition of soil organic matter and to soil-forming processes at different trophic levels (BLOCK 1984, FISCHER & SKIBA 1993). Interrelationships between soil invertebrates and non-living soil compounds in tundra systems of the Arctic and Antarctic have been summarised by HOLDGATE (1977) and VINCENT (1988).

Collembolans are widespread in the Arctic (FJELLBERG 1986) and can show a high degree of species diversity (RYAN 1981). They were noted in considerable numbers in nearly all locations (Tab. 2). They belong to the most common invertebrates of this environment and may reach numbers of $0.2\ 10^6\ m^{-2}$, and nematodes can reach counts of more than $10^6\ m^{-2}$ (MCLEAN 1981). Soils of the maritime Antarctic tundra showed the existence of up to $10^4\ m^{-2}$ nematodes and collembolans (BÖLTER et al. 1997). Enchytraeids and lumbricids could not be observed in the samples taken in this study, probably because the sampling size was not large enough.

Soil algae, cyanobacteria and fungi

It seems difficult to compare the data obtained about autotrophs from the TNW-99 study with those from other studies. One reason is that algae are mostly used for taxonomic studies via cultures and are not regarded as constituents of the microbial soil flora in its soil-ecological sense. A second point is that ecological emphasis on algae is mostly put on them as primary producers in wet areas; data from mesic or only sporadically moist places are rare. KERCKVOORDE et al. (2000) describe findings of 0.5-1.7 10^6 diatoms g^{-1} d.wt. in soils from NE Greenland. BUNNELL et al. (1975) reported that for soils in tundra near Barrow a single species of algae may account for $10^7\ g^{-1}$ soil. Colony-forming units numbered in the range 1.6-2.4 10^4 in different soils on Devon Island (JORDAN et al. 1978). Most of the autotrophs could be identified as diatoms, e.g., *Navicula* sp., comparable to the report of BUNNELL et al. (1980).

Algal numbers on plants and mosses were lower, between 10^3-10^4 cells g^{-1} d.wt. (Tab. 6). Data comparable to those found in this study were described in soils from the Russian Arctic (Taymyr Peninsula and Severnaya Zemlya) (BÖLTER & KANDA 1997, BÖLTER & PFEIFFER 1997). Other reports from Antarctic sites register figures in ranges from 10^4-10^6 algal cells g^{-1} d.wt. (BÖLTER 1996, 1997); here cyanobacteria dominated the surface soils.

Soil algae can easily dominate the soil microbial community in the upper horizon when conditions favour their growth (Tab. 6). It is noteworthy that the dominant portion of micro-autotrophs found during this study belongs to the cyanobacteria (BÖLTER 2001). BUNNELL et al. (1980) identified most of their blue-greens as *Schizothrix calcicola* and *Nostoc commune,* but such specific identifications were not possible from the data of this study. The great importance of cyanobacteria can be seen in relation to their ability in nitrogen fixation. This property is of advantage in nutrient-poor soils, and METTING (1991) regards these organisms as indicative of arid and semiarid lands. In such an environment they are also active in forming soil crusts or aggregates by their production of slimes, which is of great importance for soil stabilization (JOHANSEN 1993, WILLIAMS et al. 1995 a,b) and as a positive influence in the establishment of higher plant seedlings (ST. CLAIR et al. 1984, BELNAP 1990).

Soil fungi were seldom detected during the microscopic inspections, at least not in appreciable amounts, which suggested their lack of importance in this environment, although other fungi were observed in some places (Tab. 2). This can be regarded as surprising since fungi have been described as a most evident organism group in tundra environments (SCHMIDT & BÖLTER 2002). Their evaluation, however, is difficult and relies either on cultural techniques or on measurements of hyphal lengths. Because of the generally low incidence in most samples, such analysis was not performed during this study. It has to be mentioned that the occurrence of fungi is also more related to plants: not only free living bacteria or those associated with detritus are important for plant growth. A great variety of Arctic plants can be found associated with mycorrhizal fungi (KOHN & STASOVSKI 1994). (A more detailed study on these organisms was performed by A. Dahlberg of Lund University.)

Bacteria generally dominate the microbial scene in the soil. Their role is most significant at sites with an elevated amount of organic matter, i.e., in soils with living plant life or plant litter which provides a sufficient supply of nutrients. This de-

pendence becomes evident from the striking decrease in bacterial count and total biovolume with depth (Tab. 5). Nutrient descriptors decrease with depth and thus by definition, likewise nutrients (cf. BÖLTER et al. 2006). Comparable values of TBN, BBV, and MCV as presented here have been found in both arctic (BÖLTER 1998, BÖLTER & KANDA 1997, SCHMIDT & BÖLTER 2002) and antarctic regions BÖLTER (1995, 1996), BÖLTER et al. (1997, 1999). (Those data have been evaluated by the same method used for the TNW-99 study.)

BUNNELL et al. (1980, Tab. 8-2) estimated bacterial numbers for wet meadows in the Barrow region and found a seasonal average by direct count of 12.2 10^9 cells g^{-1} d.wt. (0-2 cm), 10.9 10^9 cells g^{-1} d.wt. (2-7 cm), and 8.1 10^9 cells g^{-1} dw (7-12cm) for wet meadows. Further, BUNNELL (1980, Tab. 8-1) calculated by converting plate counts to direct counts, yielding a range 4.6-9.8 10^9 cells g^{-1} d.wt. for individual microtopographic units. From these data he estimated biomass at between 0.92 and 1.52 g d.wt. m^{-2}. Biomass figures in our study for polygonal soils were 0.14-0.82 g m^{-2}, somewhat lower than near Barrow. Further comparisons with other data from tundra environments become speculative, as they were also obtained by recalculating colony forming units to direct counts by specific units derived from correlation patterns (e.g., PARINKINA 1974, CHERNOV et al. 1975, ROSSWALL et al. 1975), although data from the latter investigation match those from the TNW-99 study.

But it's not only the distribution of the total numbers of bacteria and their contribution to the total microbial biomass that is of interest in describing tundra soils. The varieties of bacteria and their proportions are also noteworthy. Size classification provides important information similar to differentiation into Gram-reaction or state of activity. Table 5 shows the contributions of rod-shaped bacteria versus cocci. Cocci and small rods (0.25-0.75 μm) dominate the communities generally with at least an 85 % share. In samples from depth greater than 10 cm their share grows to more than 92 %, and in these deep samples the share of the cocci's biovolume also increases significantly. Similar size-class distributions of bacteria have been described in other arctic and antarctic locations (BÖLTER 1990, 1995, BÖLTER et al. 1997, 1999, BÖLTER & PFEIFFER 1997).

It can be suspected that these small bacterial cells belong to Gram-positive groups, which also can be regarded as more resistant to osmotic stress and periods of starvation. DUNICAN & ROSSWALL (1974) report very variable ratios between Gram-positive and Gram-negative bacteria in tundra soils, depending on local environmental conditions rather than general trends. Most isolated organisms, however, were short rods, probable Gram-positive bacteria. From Tables 4 and 5 it becomes clear that locations with decreasing nutrient supply have bacterial communities with lower mean biovolume, which ranges around 0.03 μm^3. Such size implies a much lower mean bacterial weight (c. 3 10^{-14} g) than that proposed by BAKER (1970) for tundra bacteria (1.5 10^{-12} g).

The primary inspection of the soils in combination with the detailed laboratory analyses have shown that the soils are dominated by varying communities of phototrophic and heterotrophic organisms. The heterotrophic communities are strongly related to the existence of an active phototrophic layer, which may consist of higher plants or cryptogams plus soil algae. The latter group may be dominated by cyanobacteria (BÖLTER 2001). Hence, the functioning of the system can be regarded as well balanced, although the distribution of such harmonious units is small in area and/or they last for only short periods.

A clear separation between sites with or without soil phototrophs as related to other environmental properties is not possible. Sites with algae tend to show elevated bacterial counts and mean cell volumes. Algae thus can be regarded as at least stimulators of bacterial growth in nutrient-poor soils, and also as providing some storage of organic matter for less productive time spans.

Reactions over a short period of time and with a detectable change in the bacterial community remain speculative from the data obtained here. It seems to be more evident for that the bacterial community acts more in its totality by manifesting elevated numbers and biomass in correspondence with elevated organic material – albeit the latter is generally a material of a resistant sort. Hence, for survival it appears that this community has to act in steady way rather than by large and rapid fluctuations of supplies of low-weight organic material. It has been shown in other environments that metabolic processes relying on high quality substances are more sensitive to temperature than those of low quality substances because of their different activation energies (MIKAN et al. 2002, AGREN & BOSATTA 2002), which cannot be regarded as a benefit in such a system. These communities have to look for a strategy for longer survival under harsh conditions.

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