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Biomass and Enzyme Activity of Two Soil Transects at King George Island, Maritime Antarctica

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Abstract

Soil microbial properties were investigated to assess the potential of organic matter dynamics in mineral and ornithogenic soils in a cold climate. Microbial biomass, respiration, N-mineralization, and enzyme activities were measured along two catenary transects crossing penguin rookeries and seabird colonies. Ornithogenic excrements, total organic carbon (TOC), and phosphorus accumulation were major factors controlling microbial properties in Antarctic soils. Multivariate approaches (cluster and discriminant analysis) clearly distinguished the ornithogenic soils from the mineral soils based on their microbial characteristics. Microbial biomass, respiration, and N-mineralization were gradually inhibited by increasing P-inputs by penguins. The metabolic quotient (qCO_2) was negatively correlated to P-content, whereas all other microbial properties (microbial biomass, respiration, N-mineralization, enzyme activities) followed the patterns of TOC. Urease, xylanase, phosphatase, and arylsulfatase activities were significantly favored by penguin and seabird excrements in the ornithogenic soils compared to the mineral soils. Microbial biomass-to-enzyme activity ratios were substantially higher at sites influenced by penguin guano than by other seabird excrement. We show that enzymes are active in antarctic soils, and that high levels of biomass-based specific activity in the ornithogenic soils, compared to those of mineral soils, result from continuous input of large quantities of enzyme-rich penguin guano.

Introduction

Microorganisms play a key role in cycling nutrients in soils of the isolated antarctic ecosystem, where organic matter derives primarily from soil algae and slow-growing cryptogamic plants (Tibbles and Harris, 1996). Locally, penguins and other seabirds transfer large quantities of organic and inorganic material from the ocean to terrestrial antarctic ecosystems (Orchard and Corderoy, 1983; Beyer et al., 1999a), and accumulated guano deposits in the coastal rookeries are an important source of organic matter. Long periods of snow cover, low temperatures, and related low water availability represent major factors controlling microbial life in these environments.

Various investigations have focused on the environmental factors related to microbial growth, numbers, biomass, and respiration (e.g., Wynn-Williams, 1982; Bölter, 1992, 1993, 1995; Bölter et al., 1997), hydrolytic activity (Bölter, 1992), nitrogen fixation (Christie, 1987; Bölter et al., 1995), and extracellular enzyme production of isolated fungi (Ray et al., 1989; Fenice et al., 1997) in continental and maritime Antarctica. However, there is relatively little information on whether the microbial mineralization of organic compounds differs between mineral and ornithogenic soils. The latter have many features which distinguish them from other soils: bacterial production and respiration (Tibbles and Harris, 1996), bacterial numbers and viability (Ramsay and Stannard, 1986), total microbial biomass (Roser et al., 1993), and total microbial CO_2 evolution (Orchard and Corderoy, 1983) differ significantly. Roser et al. (1993) have shown that microbial biomass and microbial viability in ornithogenic soils vary with their location in continental Antarctica, maritime Antarctica, and subantarctic regions. Furthermore, enzyme activity involved in soil organic matter mineralization can be used to indicate the decomposition potential of ornithogenic soils. Only few reports are available on enzymes in mineral (e.g., Bölter, 1992; Fenice et al., 1997) and ornithogenic soils (Pietr et al., 1983; Speir and Ross, 1984; Bölter, 1992).

The objective of this study is to quantify the influence of penguin guano and seabird excrement on microbial properties of maritime antarctic soils along two catenas crossing stony moraines of different ages. The approach involves measuring microbial biomass (C and N), bacterial numbers and biomass, respiration, N-mineralization, and soil enzyme activities to assess the functional diversity of soil microorganisms in antarctic environments.

Material and Methods

STUDY AREA

King George Island is located in the climatic zone of maritime Antarctica. The annual mean temperature is −1.7°C (1977–1996), but from December to April the range of the monthly mean is from 0.9 to 2.3°C, with maximum daily temperatures of 16.7°C in January and minimum daily temperatures of −32.3°C in July (Rakusa-Suszczewski et al., 1993; Kejna, 1999). Yearly

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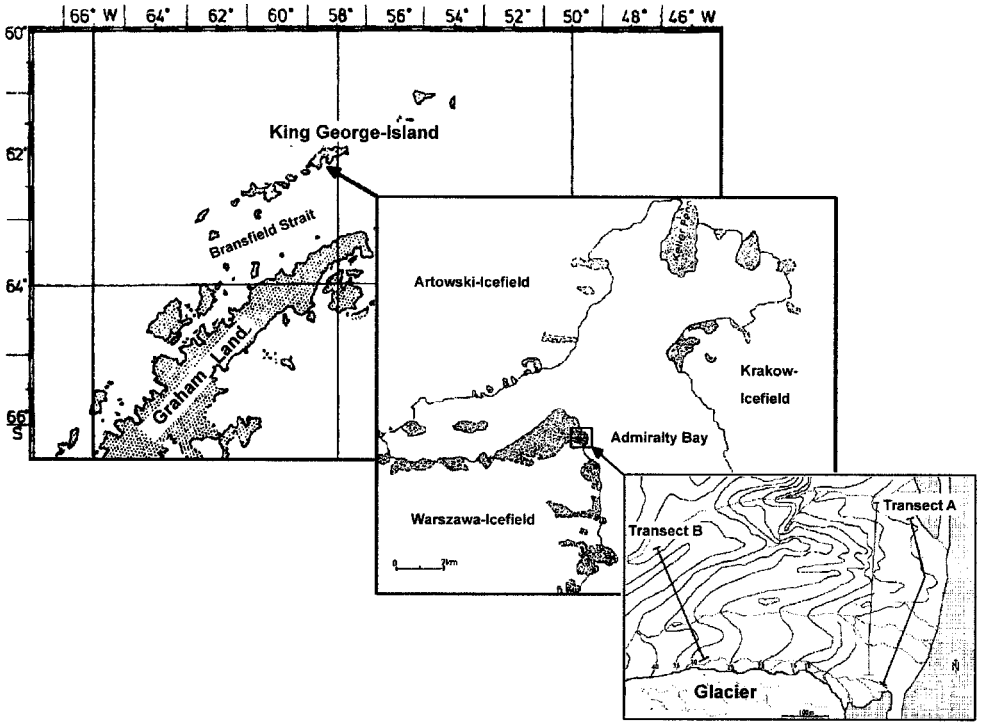

FIGURE 1. Map of Admiralty Bay region, King George Island (Kejna, 1999; Rakusa-Suszczewski, 2002, modified).

precipitation is 510 mm with a nearly homogeneous distribution over the year. In March there is an extreme minimum due to the decreasing temperature at the onset of the antarctic winter. The recent vegetation in the ice-free oasis of King George Island is characterized by mosses, some liver mosses, lichens, and algae (Olech, 1993; Zarzycki, 1993) as well as by the higher plants *Deschampsia antarctica* and *Colobanthus quitensis.* Huge areas of landscape are nonvegetated, and the occurrence of vegetation shows a high variation and an extreme patchiness.

The investigation site is located near the permanently occupied Polish Station H. Arctowski at King George Island (58°20′E, 62°10′S), located at the shore of Admiralty Bay (Fig. 1).

The parent material of soil is mainly neoglacial moraine rubble (centuries old and younger) and fluvioglacial sands influenced by eolian deposits and volcanic ash (Blume et al., 2002). Relic penguin rookeries are scattered widely within the ice-free areas (Tatur and Myrcha, 1984; Myrcha and Tatur, 1991), and active colonies are located next to the coastline. Most soils are affected by permafrost between 50 and 200 cm depth (Kuhn, 1997).

TRANSECTS

Sampling transects are described in Table 1. Soil samples were taken along two catenary soil transects perpendicular to the nearby Ecology Glacier (Kuhn, 1997: Fig. 1). They were established for botanical studies (Olech, 2002). Transect A is 10 to 20 m inland from the shore, whereas transect B is located several hundred meters farther inland. The direction of transect A is south-north, starting with site A0, about 2 m away from the glacier, and ending at site A15, 306 m north of the glacier. The direction of transect B is south-southeast to north-northwest, starting with site B1, 16 m from the glacier, and ending at site B12, 237 m from the glacier. The vegetation has been characterized along both transects (Olech, 2002). The sampling sites are located in valleys or depressions between the moraines as well as on feet, slopes, or tops of moraines. On transect A, the first visible vegetation—the grass *Deschampsia antarctica* and the moss *Polytrichum piliferum* along with certain other mosses—occurred nearly 100 m away from the glacier, although the surface coverage was still extremely low (Table 1). The lichen *Usnea antarctica* is found 200 m from the glacier, whereas the alga *Prasiola crispa* is restricted to sites A13–A15, which are characterized by a visible penguin impact (Table 1: remarks). Mosses are absent at these sites. With higher vegetation cover at distances >200 m from the glacier, *D. antarctica* becomes the dominant plant. Transect B is characterized by a similar pattern of plant occurrence with respect to the distance from the glacier (Table 1). The vegetation cover, however, is greater beginning 130 to 140 m from the glacier, and *D. antarctica* is no longer the dominant plant. Here, mosses and, at the last point (B12), *U. antarctica* have a much greater abundance. Seabird excrements are visible on moraines most distant from the glacier (B9–B12).

Soils are classified according to the International Society of Soil Science (ISSS-FAO, 1998, Table 1). Some of the sites on both transects are enriched with volcanic glass. Hence, they are classified as vitric Andosols (A7, A8, B3, B4, B6, B10) or vitric subunits of Cryosols (A6, A9, B1). Only some soils show active cryoturbation phenomena and are thus classified as Cryosols (A1, A2, A6, A9, B1, B2), whereas the others are gelic subunits of varying soil types.

SOIL SAMPLING

For reasons of environmental protection and in accordance with the Antarctic Treaty, sampling had to be restricted (UNOG, 2000). The sampling design followed the vegetational gradient along both catenary transects (A0–A15, B1–B12). A spade was used to take the soil samples from different horizons. One bulk sample of the topsoil (0–20 cm) and a subsoil sample (30–55 cm, depending on depth of soil) were taken from each site along the transects (Table 1) and stored in plastic bags at −20°C. For determinations of bacterial biomass and bacterial counts, a subsample was taken from the 0–5-cm surface layer of each site along both transects. The samples for enzymatic studies were

TABLE 1

Detailed site description of the antarctic soil profiles sampled at transects A and B on King George Island[a]

Code	Location	Depth[b] (cm)	Vegetation	Cover[c] (%)	Soil Units (ISSS-FAO 1998)	Dist.[d] (m)	Remarks
A0	gl edge	32	nil	0	Eutri-gelic Fluvisol	2	fluvio-glacial
A1	m. foot	32	nil	0	Calcari-turbic Cryosols	32	moraine
A2	m. top	30	nil	0	Calcari-turbic Cryosols	37	
A3	m. slope	35	nil	0	Eutri-turbic Cryosols	55	
A4	m. top	40	*D. ant.*	0.5	Hyposali-gelic Regosol	93	wind-protected
A5	m. valley	40	*D. ant.*, mosses	1	Vitri-gelic Fluvisol	129	fluvic
A6	m. top	45	*D. ant., Poly.*, mosses	1	Vitri-turbic-Cryosol	142	
A7	m. foot	47	*D. ant., Poly.*, mosses	1	Geli-vitric Andosol	146	
A8	m. top	50	*D. ant., Poly.*, mosses	5	Geli-vitric Andosol	167	
A9	m. slope	60	*D. ant., Poly.*, mosses	7	Vitri-turbic Cryosol	176	
A10	m. top	50	*D. ant., Poly.*, mosses	4	Eutri-gelic Regosol	188	
A11	m. top	55	*D. ant., Poly.*, mosses, *Usnea*	4	Eutri-gelic Regosol	203	
A12	depression	35	*D. ant.*	55	Dystri-gelic Regosol	221	
			Poly., mosses, *Usnea*	15			
A13	m. top	40	*D. ant*	90	Skeleti-gelic	233	20 cm[e]
			Prasiola crispa	10	Umbrisol[f]		
A14	m. top	35	*D. ant., Prasiola crispa*	100	Sali-gelic Umbrisol[f]	245	center[g]
A15	m. slope	55	*D. ant*	60	Humi-gelic	306	200 cm[e]
			Prasiola crispa	40	Umbrisol[f]		
B1	m. foot	35	nil	0	Vitri-turbic Cryosol	16	
B2	m. slope	35	nil	0	Calcari-turbic Cryosol	32	
B3	m. top	ND	*D. ant*	0.1	Geli-vitric Andosol	76	
B4	depression	40	*D. ant*	0.5	Geli-vitric Andosol	106	
B5	m. foot	50	*D. ant*	0.5	Eutri-gelic Regosol	116	
B6	depression	40	*D. ant,* mosses	3	Geli-vitric Andosol	133	
B7	m. slope	40	*D. ant.*, mosses, *Usnea*	30	Skeleti-gelic Regosol	141	
B8	depression	40	*D. ant*	15	Skeleti-gelic Regosol	181	
			Poly., mosses	65			
B9	m. foot	35	*D. ant*	10	Eutri-gelic Regosol	184	
			Poly., mosses	80			
B10	m. slope	40	*D. ant*	5	Geli-vitric Andosol	213	
			Poly., mosses	80			
			Usnea	10			
B11	m. slope	50	*D. ant*	5	Skeleti-gelic Umbrisol	231[f]	
			Poly., mosses	30			
			Usnea	25			
B12	top	50	*D. ant., Poly.*	5	Skeleti-gelic Umbrisol	237[g]	
			mosses	5			
			Usnea	90			

[a] Abbreviations: gl: glacier, m.: moraine, mosses: diverse moss species, *D. ant: Deschampsia antarctica, Poly.: Polytrichum piliferum, Usnea: Usnea antarctica.*
[b] Depth of digging (soil profile).
[c] Soil surface coverage by recent vegetation.
[d] Distance from glacier edge.
[e] Distance from abandoned seabird nests.
[f] Ignoring the high P content due to seabird impact.
[g] Center of an abandoned seabird nest.

allowed to thaw at +4°C for 3 d; those for physicochemical analyses air dried at room temperature before being sieved (<2-mm fraction) and analyzed. The total number of soil samples was 58 for microbial and chemical measurements and an additional 29 for bacterial counts and bacterial biomass.

SOIL PHYSICAL AND CHEMICAL ANALYSES

Most chemical and physical properties were determined by methods given by Schlichting et al. (1995). In brief, soil texture was determined by the sieving and sedimentation method after H_2O_2 treatment and $(NaPO_3)_6$ dispersion. Total organic carbon (TOC) and nitrogen (N_t) were measured by dry combustion at 1200°C and thermal conductivity detection. Kjeldahl digestion and subsequent colorimetric detection of NH_4^+ were used to determine total nitrogen (N_t). Exchangeable bases (BEC = Ca^{2+} + Mg^{2+} + K^+ + Na^+) were extracted by $BaCl_2$ at pH 8.2 and available phosphates (P_{citr}) by citrate solution. The pH was measured in $CaCl_2$ solution (soil-solution ratio 1:2.5), electrical conductivity (EC) in the saturation extract. Soil moisture (%ww^{-1}) was measured gravimetrically after drying at 105 °C for 24 h.

MICROBIOLOGICAL ANALYSES

Total bacterial numbers (TBN), total bacterial biomass (C_{bac}), and related parameters were determined by epifluorescence microscopy (acridine orange staining of suspensions on polycarbonate membranes, pore size 0.2 μm; Bölter, 1992,

1995). Bacteria were identified by shape and size, and biovolumes were calculated from geometrical characteristics. Biovolumes were further taken as the basis for C_{bac} by assuming a C content of 10% of total biovolume. Microbial biomass–C (C_{mic}) was indirectly determined by substrate-induced respiration (SIR) using glucose added to soil and incubation at 25°C for 4 h. The CO_2 evolved was trapped in NaOH and measured by titration (Jäggi, 1976). C_{mic} ($\mu g\ C_{mic}\ g^{-1}$ soil) was calculated as [$\mu g\ CO_2\ g^{-1}$ soil] $\times$ 20.6 $\times$ 0.847 (Jenkinson et al., 1987; Kaiser et al., 1992). Microbial biomass–N (N_{mic}) was determined by the chloroform-fumigation-extraction (CFE) and ninhydrin-reactive-N NHR-N (Amato and Ladd, 1988). N_{mic} ($\mu g\ N_{mic}\ g^{-1}$ soil) was calculated as [μg NHR-N g^{-1} soil] $\times$ 3.1 according to Amato and Ladd (1988). Microbial respiration is obtained by the titration procedure (Isermeyer, 1952; Jäggi, 1976). The CO_2 evolved was determined as described in the SIR-method. The metabolic quotient (qCO_2) is expressed as mg CO_2-C evolved $g^{-1}\ C_{mic}\ h^{-1}$.

N-mineralization was measured under 1-wk water-logged incubation (Keeney, 1982; Kandeler, 1996). Alkaline phosphomonoesterase activity (referred to in the text as phosphatase activity) was assayed by using buffered disodium phenylphosphate (0.2 M borate buffer, pH 10, 20 mM phenylphosphate) as a substrate. The released phenol was estimated colorimetrically at 400 nm (Hoffmann, 1968). Arylsulfatase activity was measured according to Tabatabai and Bremner (1970) using p-nitrophenylsulfate solution as the substrate. These enzyme assays measure p-nitrophenol colorimetrically as the reaction product. Urease activity was assayed as described by Kandeler and Gerber (1988) using urea as the substrate. Xylanase activity was determined as described by Schinner and von Mersi (1990) using 1.2% xylan as the substrate followed by colorimetric determination of the reducing sugars. All enzyme assays were done at 37°C except xylanase, which was done at 50°C.

DATA HANDLING AND STATISTICAL ANALYSIS

C_{mic}, N_{mic}, C_{bac}, respiration, and soil enzymatic activity were calculated on an oven-dry weight (105°C) basis. Ratios of enzyme activity-to-C_{mic} were calculated as indicators of the hydrolytic potential of the microbial community to break down organic material. For simplicity, we refer to the enzyme activity-to-C_{mic} ratio as specific enzyme activity. All parameter measurements were tested for normality (Kolmogorov-Smirnov Goodness of Fit test) and homogeneity of variances (Levene's test). Normal distribution of the data was obtained after log-transformation of all data. The classification of the investigated sites based on nine variables (microbial biomass C and N, respiration, N-mineralization, metabolic quotient, enzyme activities) and the subsequent relation of the classification to ornithogenic impact was carried out by cluster analysis using standardized data, Euclidean distance as a measure of dissimilarity, and the centroid method as the agglomeration algorithm. In order to determine whether the ornithogenic impact levels at the sites can be identified by their microbiological properties and what the discriminatory importance of each microbial variable is, discriminant function analysis was applied. The groups were defined according to the ornithogenic impact, transect and soil depth. Multivariate Wilks' Lambda was used for the stepwise selection of the variables. Differences of means of microbiological variables between ornithogenic and mineral soils were tested by univariate analysis of variance using ornithogenic impact as the main factor and P_{citr}, TOC, and P_{citr} as covariates, followed by the multiple range test (Student Newman Keuls test). The relationship between TOC, P_{citr} content, pH, and soil microbial parameters was tested by partial correlation analyses where parameters other than those to be tested were controlling factors.

Results

CHEMICAL AND PHYSICAL CHARACTERISTICS OF THE ANTARCTIC SOIL

Most investigated soils are enriched with gravel and stones, reflecting the special conditions of the parent material (moraines). The dominant soil texture is sandy loam (Table 2) with clay contents up to 20%. Abrupt textural changes between top- and subsoil within one profile occur at A4 and A9 due to the mixing of differently textured sedimentary deposits during glacial transports (Blume et al., 1997; Kuhn, 1997).

The soils (A0–A11, B1–B6) on young moraines (10 to 30 yr) have nearly no vegetation cover, carbonate contents of up to 2.9 g kg^{-1}, and are almost free of organic matter (TOC $<$2 mg kg^{-1}, Table 2). By contrast, soils (A12–A15, B7–B12) on older moraines (hundreds of years old) are strongly acidified (pH $<$ 5) and enriched with organic matter. These soils show carbonate loss, acidification, and base desaturation together with organic matter accumulation, processes which occur very quickly on soils with high nutrient reserves (due to basaltic origin) and rapidly growing vegetation cover.

Nitrogen compounds are only found in trace amounts (0.10–2.86 g kg^{-1}) in ornithogenically influenced soils (A13–A15, B9, B11–B12). For soils with N concentrations close to detection limits, the C/N ratios are not calculated (A0–A12, B1–8, B10). Along with an increasing occurrence of vegetation and/or the impact of bird excrement, the TOC and N_t contents in the topsoils also greatly increase. At transect A, narrow C/N ratios (4.8–6.7) confirm the penguin impact at site A13–A15. This is in line with data from other areas in Antarctica (see reviews: Campbell and Claridge, 1987; Beyer et al., 1999a), which show such ornithogenic soils to be characterized by C/N ratios of 5 or lower.

The base exchange capacities (BEC), which characterize the released and bound nutrients (Ca, Mg, K, Na), are lowest at the far ends of both transects, which show lowest pH levels (Table 2). However, the constant decline of pH values with increasing distance from the glacier is not reflected by the BEC, probably due to increasing TOC levels, textural and mineral differences of the soil matrix, and the parent materials (Kuhn, 1997).

ORNITHOGENIC SOILS IN ANTARCTICA

In antarctic environments penguins and seabirds play an important role in soil development. Tops of the old moraines are covered by penguin guano (A13–A15) and seabird excrement (B9–B12). The influence of penguins and seabirds has resulted in a strong enrichment of phosphate. Guano and bird excrement enrich soils with organic nutrients (e.g., proteins, urea), which can be mineralized and transformed into nitric and sulfuric acids. This causes extremely low pH at bird nests and sites downslope of the nests (A15). The acidification results in elevated levels of oxalate-extractable iron from basaltic rocks, showing high contents of easily weatherable pyroxenes (Blume et al., 2002). Some soils are characterized by medium to high electrical conductivity due to the influence of guano excrement (A13–A15) (Table 2).

CLASSIFICATION OF ORNITHOGENIC SOILS ACCORDING TO MICROBIAL PROPERTIES

The dendrogram of the cluster analysis, based on microbial biomass and enzyme activity data, displays an unequivocal re-

TABLE 2

Selected soil properties at transects A and B[a]

Code	Distance m	Texture	TOC g kg^{-1}	P_{citr} mg kg^{-1}	pH $CaCl_2$	EC mS	BEC $cmol_c$ kg^{-1}
A0/1	2	M.SL	1.37	178	6.7	2.4	14.0
A0/2	2	M.L	1.16	443	6.7	4.9	15.8
A1/1	32	A.SL	0.77	339	6.7	0.4	12.3
A1/2	32	M.SL	0.68	475	6.7	0.3	13.8
A2/1	37	M.SL	0.92	386	6.8	0.4	15.5
A2/2	37	M.L	0.64	585	6.8	0.3	14.1
A3/1	55	M.L	1.01	488	6.3	0.2	16.2
A3/2	55	M.L	0.97	382	6.6	1.3	12.8
A4/1	93	M.MS	0.98	161	6.5	5.9	12.0
A4/2	93	M.SL	0.95	384	6.5	0.7	12.5
A5/1	129	M.CS	0.79	193	6.5	1.0	10.8
A5/2	129	A.LCS	0.85	180	6.7	1.5	12.6
A6/1	142	A.LCS	1.19	280	7.2	0.9	13.8
A6/2	142	A.LCS	1.02	152	7.2	0.3	10.9
A7/1	146	A.LCS	1.41	241	6.6	0.6	13.8
A7/2	146	A.CS	1.00	161	6.6	0.5	10.9
A8/1	167	M.SL	2.05	434	6.6	0.8	31.2
A8/2	167	M.SL	1.18	293	6.6	0.6	20.6
A9/1	176	M.LCS	1.88	362	6.4	0.8	15.1
A9/2	176	M.SL	1.86	415	5.9	0.7	24.5
A10/1	188	M.L	1.60	519	6.6	1.3	20.3
A10/2	188	M.SL	1.34	339	6.6	0.6	18.7
A11/1	203	M.SL	1.91	442	5.9	0.5	32.0
A11/2	203	A.SL	1.32	437	5.9	0.5	26.4
A12/1	221	M.SL	1.80	368	4.0	8.6	15.3
A12/2	221	M.SL	1.28	237	4.0	1.3	24.2
A13/1	233	M.SL	6.25	2188	4.7	5.2	17.2
A13/2	233	A.SL	0.68	329	5.9	0.9	11.6
A14/1	245	A.SL	9.31	2678	4.4	23.0	13.8
A14/2	245	M.LCS	2.03	635	4.0	5.1	4.6
A15/1	306	M.SL	19.26	9180	3.5	2.3	9.9
A15/2	306	M.SL	6.79	3458	3.5	3.6	6.6
B1/1	16	C.L	1.34	400	6.7	0.4	20.9
B1/2	16	M.L	2.61	449	6.8	0.8	21.4
B2/1	32	C.SL	1.93	331	6.8	0.6	17.7
B2/2	32	M.L	0.93	480	6.7	0.3	20.4
B3/1	76	M.L	1.89	355	6.8	0.7	21.3
B3/2	76	M.SCL	1.21	423	6.8	0.5	20.6
B4/1	106	M.L	1.20	398	6.7	0.3	19.1
B4/2	106	M.SL	0.92	292	7.5	1.9	16.0
B5/1	116	C.SIL	1.04	220	6.4	0.7	18.4
B5/2	116	C.SL	0.66	185	6.4	0.6	18.1
B6/1	133	A.SCL	0.91	381	6.7	0.2	20.2
B6/2	133	A.SL	0.87	384	7.0	1.2	19.5
B7/1	141	M.SL	0.69	390	6.0	0.5	18.6
B7/2	141	M.SL	0.58	393	6.3	1.2	19.5
B8/1	181	A.LCS	1.84	436	5.7	0.2	13.2
B8/2	181	A.CS	0.39	182	5.7	0.4	9.4
B9/1	184	M.SL	5.15	1066	5.7	0.2	14.2
B9/2	184	M.SL	1.32	667	5.7	0.3	16.8
B10/1	213	C.SL	4.79	658	4.6	0.3	16.6
B10/2	213	C.SL	0.60	411	4.1	0.7	16.7
B11/1	231	M.SL	8.81	1877	4.9	0.6	8.4
B11/2	231	A.SL	0.52	424	6.9	0.9	17.9
B12/1	237	M.SL	22.00	759	4.3	0.8	9.9
B12/2	237	A.SL	1.81	671	4.6	0.6	2.1

[a] Abbreviations: Texture: gravel (vol%)—C common 5–15, M many 15–40; A abundant 40–80; fine soil (<2 mm)—S sand (F fine, M medium, C coarse), SL sandy loam, L loam, LCS loamy clay sand, SCL sandy clay loam, SIL silt loam (FAO, 1990), TOC total organic carbon, EC electrical conductivity, BEC base exchange capacity, (./1: 0–20 cm, ./2: 30–55 cm).

sult: soils influenced by penguin guano or seabird excrement (A13–A15, B9–B12) are clearly distinguished from the mineral soils (A0–A12, B1–B8) (Fig. 2). At the first level of clustering the ornithogenic topsoil B10 is separated from all other sites, showing highest levels of microbial biomass and enzyme activity. This may reflect the low P_{citr} concentration at B10 compared to the other ornithogenic sites B9, B11, and B12, while all other chemical properties are similar. At the second level of clustering the ornithogenic topsoils are separated from the ornithogenic subsoils and the mineral soils. Only one mineral site (A12) is misclassified into the ornithogenic topsoil cluster. This site belongs to the older moraines (A13–A15) and has a more rapidly growing vegetation cover and soil development than the mineral soils of the younger moraines (A0–A11). It is therefore more similar to the ornithogenic sites A13–A15. While at the third to fifth step of clustering the ornithogenic topsoils are clustered according to their location (transect A and B), the mineral soils and ornithogenic subsoils are not grouped with respect to their ornithogenic impact, location (transect A, B), or soil depth (topsoil, subsoil). We summarize that the effect of penguin guano and bird excrements on soil microbial properties is only evident in the topsoils, whereas the subsoils of ornithogenically affected soils do not differ from the mineral soils.

DISCRIMINANT ANALYSIS

Discriminant function analysis reveals a similarly distinct pattern. Along discriminant axis 1 there is a highly significant discrimination between ornithogenic and mineral soils irrespective of transect and soil depth (Fig. 3). Discriminant function 1 (DF 1) explains 76% of the total variance of the data set and is dominated by N-mineralization (Table 3). Because of the high eigenvalue of DF 1, N-mineralization is the most important variable in discriminating ornithogenic from mineral soils, followed by N_{mic} and urease activity. DF 2, which is dominated by the metabolic quotient, explains 12% of the variance and is mainly responsible for the discrimination between transect A and transect B of the ornithogenic soils. Within the mineral soils there is neither a significant differentiation between transects nor between soil depths (topsoil, subsoil). DF 3 explains only 7% of the variation, and the highest correlation coefficient between the microbial variable and the canonical discriminant function is found for phosphatase activity. DF 4–7 cover the remaining 5% of the total variance of the data set and are not important for the discrimination of the data ($P > 0.05$).

Discriminant functions are used to classify the soils into 8 groups (ornithogenic topsoil, ornithogenic subsoil, mineral topsoil, and mineral subsoil of transect A and B, respectively). On the basis of 9 microbiological variables (microbial biomass C and N, respiration, N-mineralization, metabolic quotient, 4 enzyme activities), 100% of the ornithogenic topsoils and only 29% of the ornithogenic subsoils are correctly classified according to ornithogenic impact and transect location. Seventy-one percent of the ornithogenic subsoils are grouped into the mineral soils, and 70–75% of the mineral soils are discriminated according to transect location (A, B) and soil depth (topsoil, subsoil). On that basis soils influenced by penguin guano and seabird excrements are termed ornithogenic soils, while undisturbed sites are termed mineral soils.

ANALYSIS OF VARIANCE

The influence of penguin guano and seabird excrements on each microbial parameter is tested by univariate analysis of var-

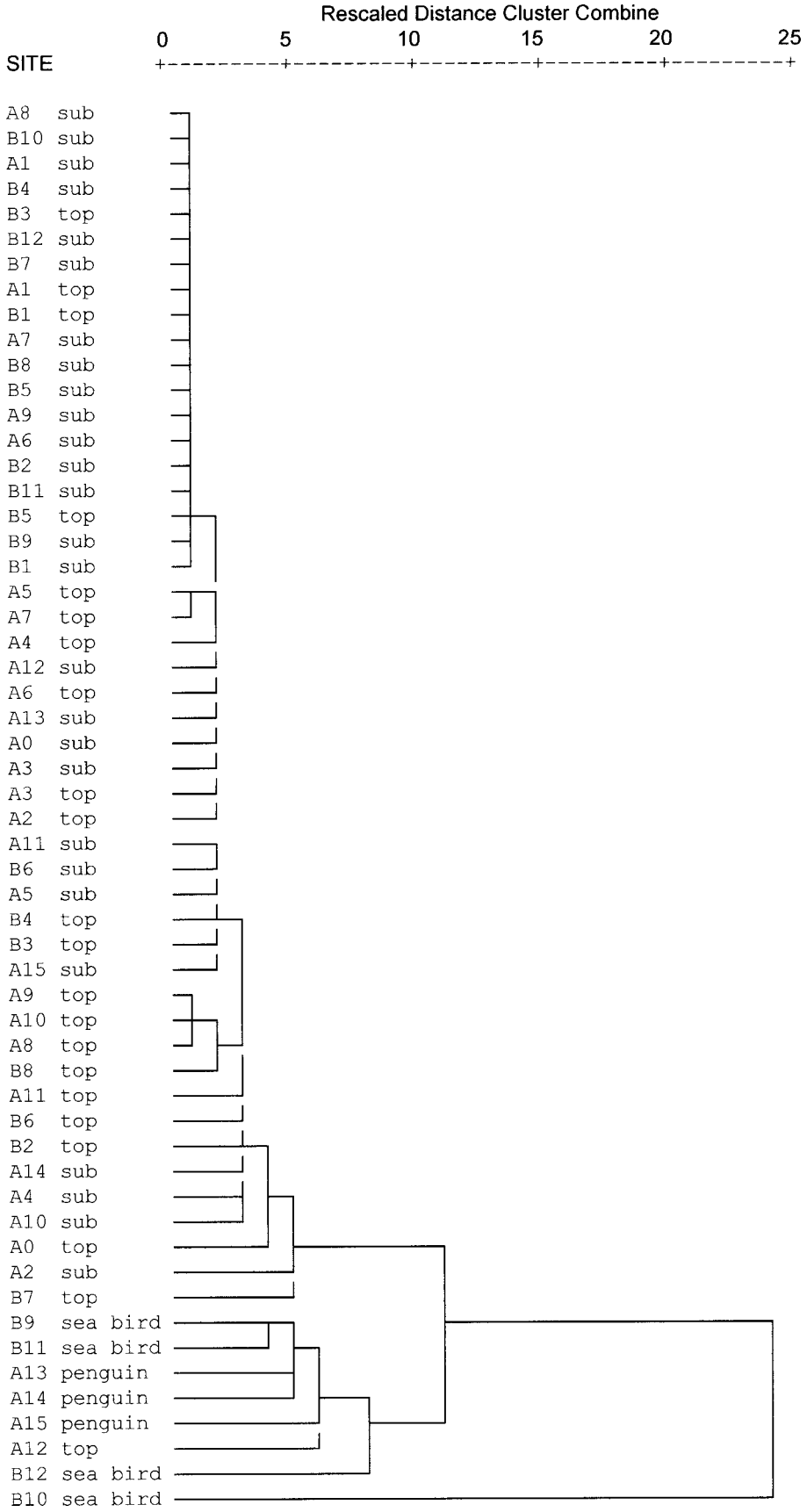

FIGURE 2. Compositional relationship among antarctic soils differing in extent of ornithogenic impact and soil depth. Dendrogram classifies the 56 sites according to their ornithogenic impact. A = transect A, B = transect B, top = topsoil, sub = subsoil, penguin = ornithogenic topsoil transect A, seabird = ornithogenic topsoil transect B.

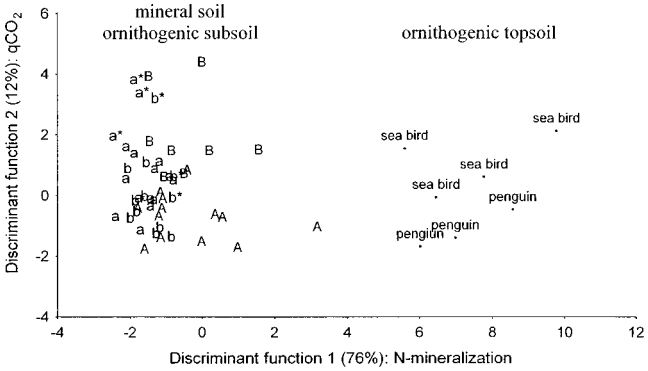

FIGURE 3. Two-dimensional plot (DF1, DF2) of discriminant analysis including all microbial variables. The discriminant analyses included data of transect A and B, two depths, and mineral and ornithogenic soils. Groups are defined according to transect location (transect A, B), ornithogenic impact (ornithogenic, mineral soil), and soil depth (top-, subsoil). Penguin = ornithogenic topsoil transect A, A = mineral topsoil transect A, a = mineral subsoil transect A, a = ornithogenic subsoil transect A, seabird = ornithogenic topsoil transect B, B = mineral topsoil transect B, b = mineral subsoil transect B, b* = ornithogenic subsoil transect B.*

iance including TOC, pH, and P_{citr} as covariates (Table 4). The analysis reveals that all measured microbial variables are significantly favored by ornithogenic excrement input, except qCO_2. Microbial biomass (C_{mic}, N_{mic}, C_{bac}, TBN), respiration, N-mineralization, and enzyme activities of the ornithogenic soils are up to 2 orders of magnitude higher compared to the mineral soils (Figs. 4, 5, 6). Differences of qCO_2 between the two soils are less pronounced, a significant difference being detected only within transect A, where qCO_2 values are 10-fold lower in the ornithogenic soils. Differences between transects are only found for N_{mic}, N-mineralization and phosphatase activity in the ornithogenic soils. Covariance analysis reveals that the ornithogenic impact as a main factor contributes 99% to explained variance, whereas the importance of the covariates TOC, P_{citr}, and pH is small. A significant influence of the covariates is detected only for N_{mic}, qCO_2, N-mineralization, and phosphatase activity (Table 4), albeit explained variance is below 11%.

RELATIONSHIP BETWEEN SOIL CHEMICAL AND MICROBIOLOGICAL PARAMETERS

Partial correlation analysis tests the relationship between microbial data sets and soil pH, P_{citr}, and TOC distribution (Table 5). A distinct pattern emerges: all microbial parameters, except qCO_2, are significantly correlated with TOC, if P_{citr} and pH are controlling factors. P_{citr} is correlated only with qCO_2, while soil pH shows no relationship to microbial variables. The results show that the microbial parameters are related to TOC, if the influence of P_{citr} and pH is considered. Otherwise, no linear relationship between chemical and microbial variables can be detected, although a quadratic model fits the data (data not shown).

SPECIFIC ENZYME ACTIVITY

Specific enzyme activity (biomass-based enzyme activity) is calculated to determine whether the ratio between enzyme activity and microbial biomass changes according to ornithognenic impact. Specific urease activity and specific xylanase activity are up to 2 orders of magnitude higher at the center of penguin rookeries or bird nest colonies compared to mineral soils, indicating significant ornithogenic impact by excrements (Fig. 6). Specific phosphatase activity shows a similar pattern, although the differences between the two soils are not significant due to the heterogeneity of the data. A significant difference is only detected between top- and subsoils. Specific arylsulfatase activity does not show any pattern, neither between ornithogenic and mineral nor between top- and subsoil (Fig. 6).

TABLE 3

Results of discriminant analyses of the microbial variables (C_{mic}, N_{mic}, respiration, qCO_2, N-mineralization, alkaline phosphatase, arylsulfatase, urease, and xylanase activity) from soils of transect A and B with two levels of ornithogenic impact

	Discriminant Function Analyses		
	DF 1	DF 2	DF 3
Wilks' lambda	0.12	0.13	0.31
Eigenvalue	9.26	1.50	0.79
Degree of freedom	63	48	35
Cumulative variance %	76	88	95
Canonical correlation coefficient[a]	0.95	0.76	0.66
Correlation coefficient[b]			
N-mineralization	0.72	−0.29	0.27
N_{mic}	0.69	0.01	−0.20
Urease	0.68	0.01	0.04
Xylanase	0.46	−0.04	0.40
Phosphatase	0.59	0.07	0.60
qCO_2	−0.183	0.39	0.08
Arylsulfatase	0.43	−0.10	−0.22
C_{mic}	0.48	0.11	−0.25
Basal respiration	0.33	0.21	−0.20

[a] Significance in the model $P < 0.05$.

[b] Denotes pooled within-group correlation between the discriminating variables and the canonical discriminant functions.

Discussion

MICROBIAL BIOMASS INDICATORS

Measured C_{mic} values are in the range of data for soils from continental Antarctica (Roser et al., 1993), but about 10-fold

TABLE 4

Results of analyses of variance (Student-Newman-Keuls-test) using the ornithogenic impact as main factor and P_{citr}, TOC, and pH as covariates. Given are F*-values and significance of difference between mineral and ornithogenic soils and of covariates*[a]

	Analysis of variance			
	Main Factor: Ornithogenic Impact	Covariates		
		P_{citr}	TOC	pH
C_{mic}	5.74***	1.72	0.60	0.91
N_{mic}	10.42***	<0.01	0.10	7.52**
C_{bac}	10.16***	0.02	0.05	7.23*
TBN	6.60**	1.70	0.03	3.39
Respiration	2.63*	1.84	0.98	1.74
qCO_2	6.53***	7.00*	11.42**	<0.01
N-mineralization	10.86***	2.24	0.53	9.80**
Urease	7.64***	1.05	0.92	3.64
Phosphatase	9.30***	0.23	0.40	4.14*
Xylanase	4.38***	2.25	3.45	3.83
Arylsulfatase	5.28***	1.50	0.13	0.06

[a] Level of significance $P \leq 0.05$ (*** $P < 0.001$, * $P < 0.01$, * $P \leq 0.05$).

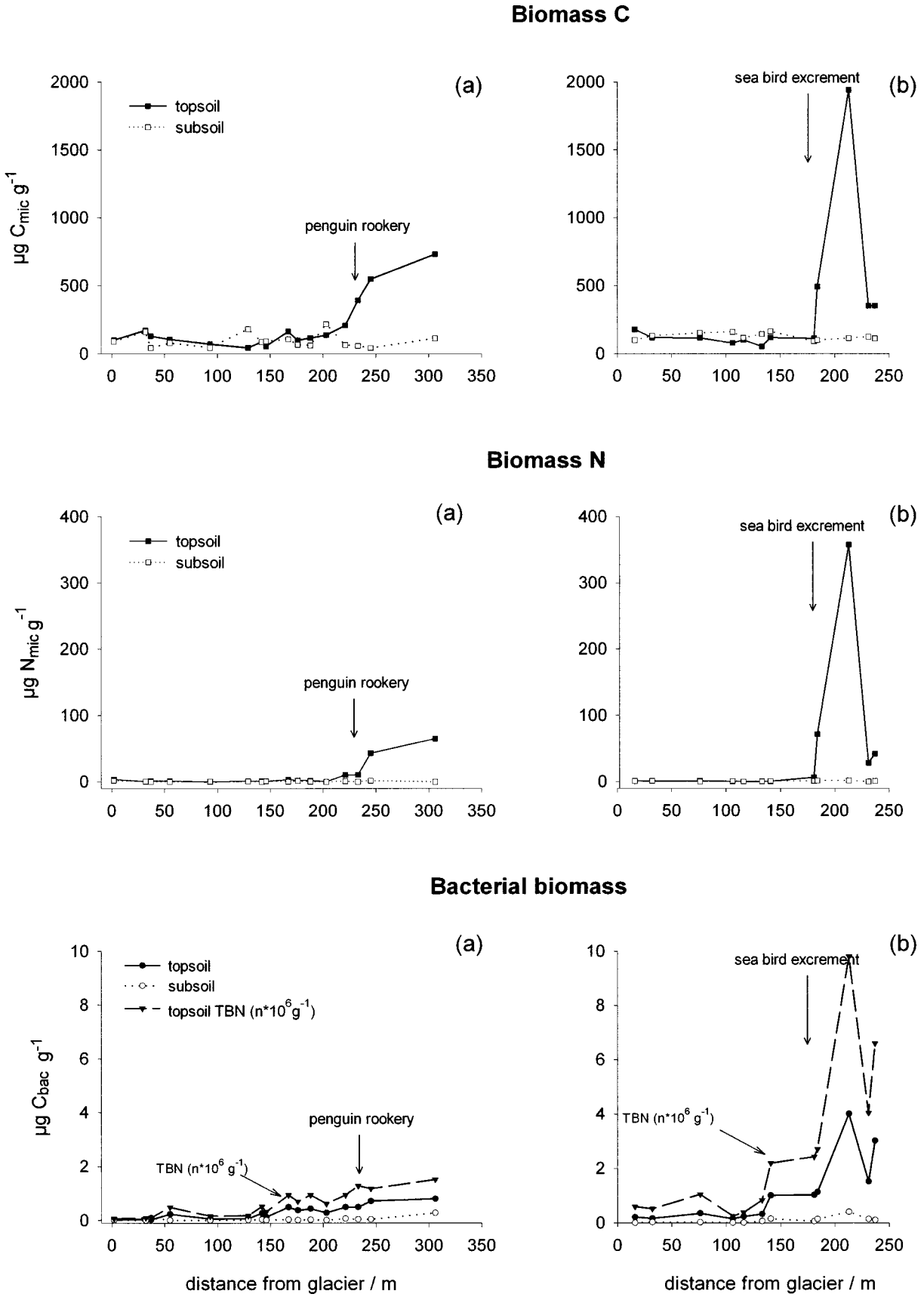

FIGURE 4. Total microbial biomass (C_{mic}, N_{mic}), bacterial biomass (C_{bac}), and bacterial numbers (TBN) at different distances from the glacier along (a) transect A, and (b) transect B. Arrow indicates the distance at which ornithogenic soils begin.

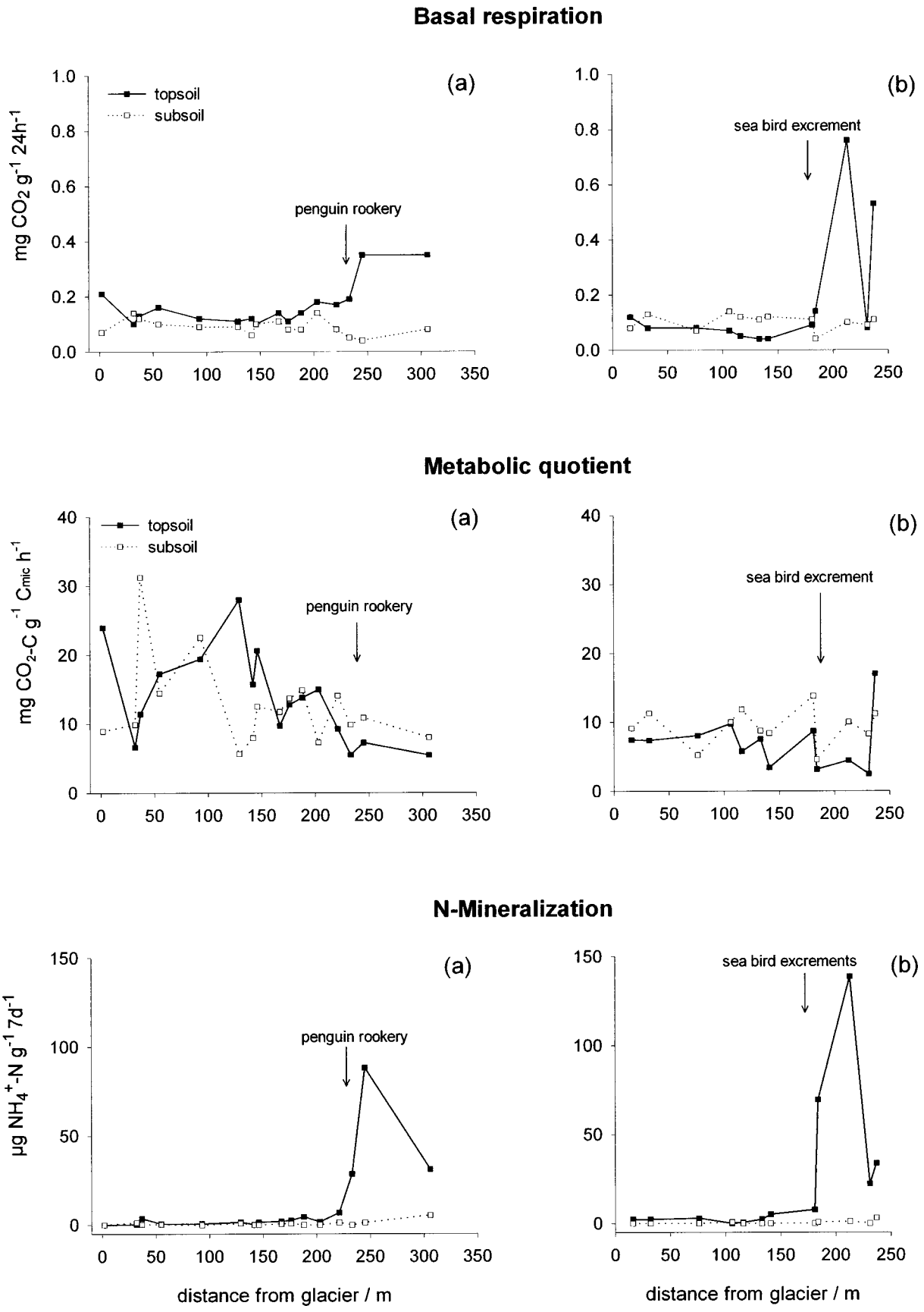

FIGURE 5. Microbial respiration, metabolic quotient, and N-mineralization at different distances from the glacier along (a) transect A and (b) transect B. Arrow indicates the distance at which ornithogenic soils begin.

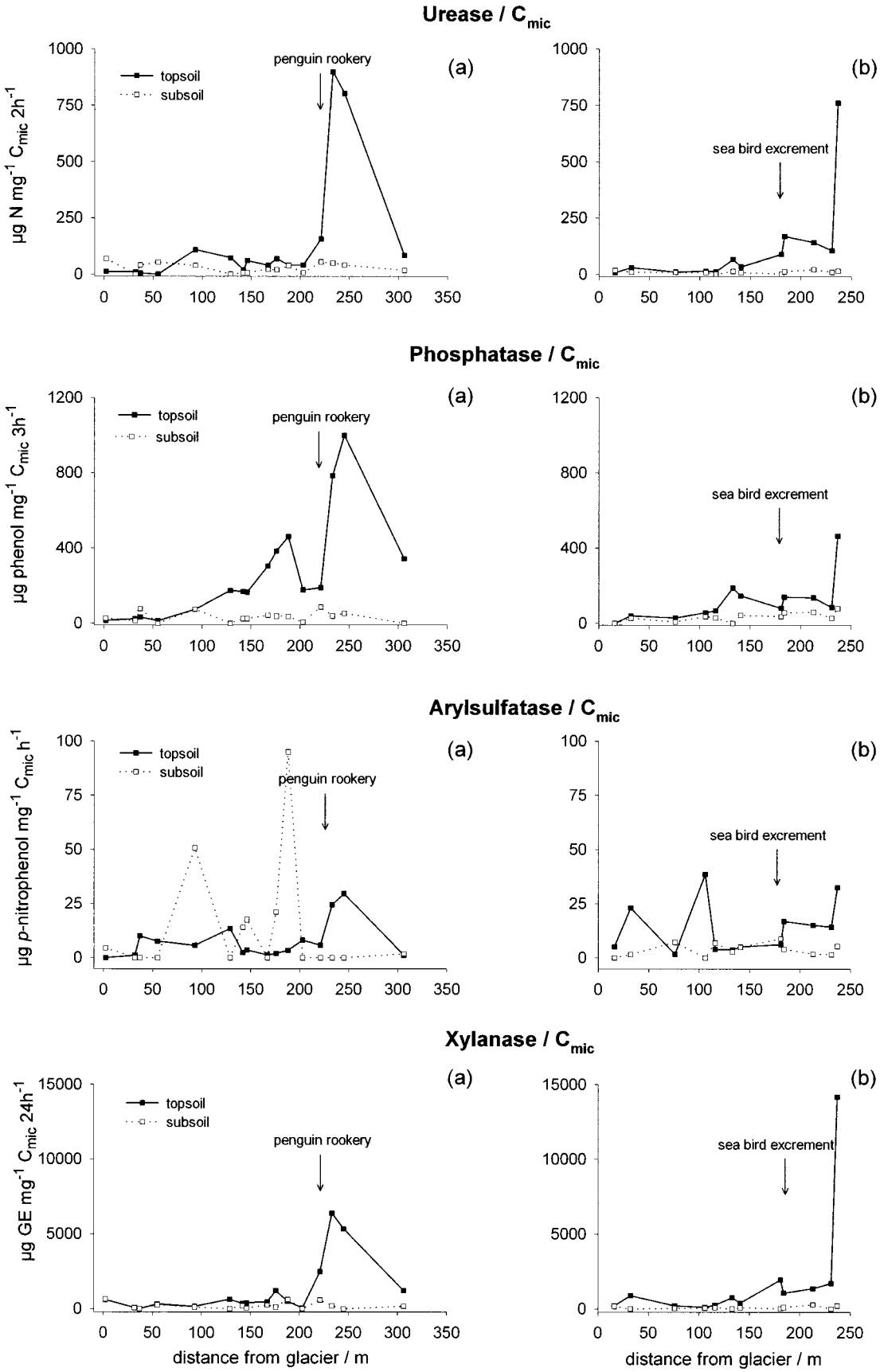

FIGURE 6. Specific enzyme activities (urease/C_{mic}, phosphatase/C_{mic}, arylsulfatase/C_{mic}, xylanase/C_{mic}) at different distances from the glacier along (a) transect A and (b) transect B. Arrow indicates the distance at which ornithogenic soils begin.

TABLE 5

Result of partial correlation analysis between P_{citr}, TOC, pH, and microbiological variables. Given are partial correlation coefficients and level of significance.[a]

	Partial correlation analysis		
	TOC[b]	P_{citr}[c]	pH[d]
C_{mic}	0.42**	0.13	0.07
N_{mic}	0.60***	−0.13	−0.11
C_{bac}	0.46*	−0.32	−0.28
TBN	0.30	−0.03	−0.18
Respiration	0.53***	−0.25	−0.07
qCO_2	<0.01	−0.30*	−0.07
N-mineralization	0.56***	0.05	−0.15
Urease	0.62***	−0.08	−0.10
Phosphatase	0.44**	−0.02	−0.08
Xylanase	0.63***	−0.24	−0.08
Arylsulfatase	0.52***	−0.15	0.07

[a] Level of significance: $P \leq 0.05$ (*** $P < 0.001$, ** $P < 0.01$, * $P \leq 0.05$).
[b] Controlling for P_{citr}, pH.
[c] Controlling for TOC, pH.
[d] Controlling for TOC, P_{citr}.

lower than levels normally observed in temperate soils (cf., Tabatabai and Bremner, 1969; von Mersi et al., 1992). However, other observations of TBN and C_{bac} in maritime (Tearle, 1987; Bölter, 1995; Bölter et al., 1997) and continental Antarctica (Ramsay and Stannard, 1986; Bölter, 1992, 1993) show quantities about 2 orders of magnitude larger (10^8–10^{10} n g^{-1}) than those found in the study area. Our results show that the quantity of microbial biomass (C_{mic}, N_{mic}, C_{bac}, TBN) in antarctic soil is primarily controlled by ornithogenic impact. Penguin guano and seabird excrements boost microbial biomass up to 2 orders of magnitude. Cofactors such as TOC, pH, and P_{citr} were less significant, only N_{mic} and C_{bac} being significantly influenced by soil pH. This could indicate a shift in the microbial community from a more bacterial- to a more fungal-dominated community with decreasing pH along the transects. The observed pattern of C_{mic} is consistent with that in Roser et al. (1993), who record C_{mic} (SIR) values between 54 μg C_{mic} g^{-1} (control sites) and 6700 μg C_{mic} g^{-1} (active penguin site) in continental Antarctica. Also, the TBN and C_{bac} results are similar to those reported in previous studies of continental Antarctica (Roser et al., 1993; Tibbles and Harris, 1996), which shows that ornithogenic soils possess more C_{bac} and TBN than sites distant from penguin colonies. The 2 to 3 orders of magnitude higher microbial biomass (C_{mic}, N_{mic}, C_{bac}, and TBN) in the ornithogenic soils of both transects can be explained by the positive influence of TOC (from vegetation cover and bird excrements). Accordingly, these parameters are closely correlated, if the influence of P_{citr} and pH is considered (Table 5) though the beneficial effect of high TOC versus the inhibitory effect of high P_{citr} and low pH levels does not allow microbial biomass to increase constantly. It seems likely that along transect A C_{mic}, N_{mic}, C_{bac}, and TBN are negatively affected by P_{citr} levels of >9000 mg kg^{-1} (A15), compared to sites where P_{citr} contents are below 3000 mg kg^{-1} (A13, A14). Within the ornithogenic soils of transect B, P_{citr} concentrations of >700 mg kg^{-1} (B9, B11, B12) reduce C_{mic}, N_{mic}, C_{bac}, and TBN. These results contradict those of Ramsay and Stannard (1986), who report higher TBN levels in active versus abandoned penguin colony sites at Cape Bird, Ross Island. Similar observations on microbial biomass have been reported at Windmill Islands in continental Antarctica (Roser et al., 1993). The authors of both studies, however, do not explicitly relate their results to the P_{citr} content of the soil. The present study suggests that ornithogenic excrements favor microbial biomass by input of substrate and nutrients, until accumulating P_{citr} becomes inhibitory on microbial growth.

RESPIRATION AND METABOLIC QUOTIENT (qCO_2)

While respiration is generally in the low range, qCO_2 is as much as 10-fold higher than normally reported for temperate soils (Insam and Haselwandter, 1989; Insam and Öhlinger, 1995). Guano and seabird excrements significantly affected the respiratory activity by substrate input, raising respiration up to 5-fold. The favoring effect can be related to the increase of TOC (Table 5), which is mineralized by microorganisms. These observations are in line with Orchard and Corderoy (1983), who report the highest microbial activity in fresh guano samples compared to abandoned rookery sites at Ross Island, continental Antarctica. As the qCO_2 is an indirect measure of a microbial community's energetic efficiency, the reported levels indicate a low metabolic efficiency of microorganisms in using organic substrates. The high qCO_2 at low TOC levels in the antarctic soils indicates a rapid turnover of organic compounds (Bölter, 1992). Differences in qCO_2 between mineral and ornithogenic sites can be explained by bird impact, TOC and P_{citr} (Table 4). The qCO_2 of the ornithogenic soils is lower, suggesting more favorable conditions for incorporating nutrients into the cell and/or a higher proportion of dormant microbial biomass (Ohtonen et al., 1999). The qCO_2 is negatively related to P_{citr} (Table 5), indicating a higher energetic efficiency with increasing P_{citr} values. Our results show that turnover rates of organic matter are high, but efficiency of the microbial turnover is low.

N-MINERALIZATION

The low rates of N-mineralization in the mineral versus temperate soils (Öhlinger, 1993; Kandeler et al., 1999a) indicate a severe deficiency of degradable organic N-compounds, evident in the low TOC levels (<2 mg g^{-1}). Accordingly, a significant correlation between TOC and N-mineralization is detected (Table 5). Within the ornithogenic sites, organic matter input (high in TOC, N, and P) by penguins and seabirds favors N-mineralization up to 25-fold rates, which correspond to levels in temperate soils (Öhlinger, 1993; Kandeler et al., 1999a). Highest N-mineralization rates are found at ornithogenic sites (A14, B10) high in TOC (>7 mg kg^{-1}) but relatively low in P_{citr} (<700 mg kg^{-1}). However, levels of >9000 mg P_{citr} kg^{-1} (transect A) and >1000 mg P_{citr} kg^{-1} (transect B) apparently inhibit N-mineralization independently of TOC. N-mineralization turned out to be the main factor for discrimination between ornithogenic and mineral soils (Fig. 3). One explanation is that actual mineralization rates are directly influenced by recent input of organic material.

SOIL ENZYMES

Along both transects, a striking feature is the high enzyme activity near recent penguin rookeries (A13–A15) and seabird colonies (B9–B12). For the specific enzyme activities, however, this pattern is only pronounced for penguin sites along transect A, which have thick guano layers, while in samples from transect B, these activities show weak ornithogenic impact (B9–B12), indicating less input of fecally derived enzymes by seabirds.

Urease activity rates are at least 1 order of magnitude lower compared to temperate soils (Kandeler et al., 1994; Kandeler et

al., 1999a). Urease activity increases along both catenary soil transects with increasing TOC levels. Accordingly, a positive correlation with TOC levels is detected (Table 5). The rates in the ornithogenic soils are at least 1 order of magnitude higher than in the mineral soils. These observations are in line with those reported for continental Antarctica (Speir and Ross, 1984), i.e., urease activity is stimulated by urea from penguin excreta at current penguin sites. The extremely high specific urease activity in the penguin rookeries (up to 1000 $\mu g\ N\ mg^{-1}\ C_{mic}$) indicates that urease may not only be microbially derived, but also derived from penguins (Fig. 6). Specific urease activity along transect B shows a less pronounced response to seabird colonies, but reflects TOC contents of the soil. At penguin sites, urease is probably derived from mircrobes and penguin guano, whereas the activity of urease per unit microbial biomass is not promoted by seabird excreta.

As phosphatases are involved in cycling of organic P-compounds, activity rates are substantially affected by ornithogenic excrements. Alkaline phosphatase exhibits 2 orders of magnitude greater activity in the ornithogenic versus mineral soils. The different activities are explained mainly by ornithogenic impact (e.g., organic P input), and secondly by the soil pH (Table 4). These results are corroborated by Pietr et al. (1983) and Speir and Ross (1984), who report organic P inputs near and on penguin sites. Similar patterns are reported for soils in continental Antarctica (Speir and Ross, 1984). Beyond ornithogenic impact, TOC influences phosphatase activity (Table 5). The mineralization of soil organic phosphorus is therefore intimately associated with the mineralization of organic matter as a whole. Specific phosphatase activity also responds to ornithogenic impact. Highest specific activities are measured in the center of the rookery, followed by the sites 20 cm and 200 cm away. No impact of bird excrement on phosphatase is detected at transect B (Fig. 6). In contrast to urease and xylanase activity, which are relatively high, alkaline phoshatase activity is generally in the low range compared to temperate soils. As phosphatases are inducible enzymes that are produced largely under conditions of low phosphorus availability and strongly inhibited by inorganic phosphates (Speir and Ross, 1978), high P_{citr} concentration may have limited phosphatase activity in the ornithogenic soils.

Arylsulfatase activity in the antarctic soil is at least 2 orders of magnitude lower than in temperate soils (Fig. 6). This activity is promoted by penguin guano and seabird excrements, showing 2-fold higher values at ornithogenic versus mineral sites. As arylsulfatase is crucial in mineralizing organic matter, it can be related to TOC concentrations (Table 5) (Speir and Ross, 1978). Arylsulfatase activity is detectable in most of the samples, but values are remarkably low. As inorganic phosphorus inhibits sulfatases (Dixon and Webb, 1979), the high P_{citr} concentrations probably reduced arylsulfatase activity here. Additionally, inorganic S-compounds from excrement may inhibit arylsulfatase activity (Speir and Ross, 1984). Specific arylsulfatase activity shows no response to penguin and seabird impact, indicating no stimulation of arylsulfatase activity by fecal material (Fig. 6).

Xylanases play a role in the biological cycling of carbon and thus respond to organic C addition into the soil (Kiss et al., 1978). At a threshold of 5 mg TOC g^{-1}, soil xylanase activity approaches levels usually reported for temperate soils (Zechmeister-Boltenstern et al., 1991; Kandeler and Eder, 1993). Penguin and seabirds had a substantial effect on xylanase activity. The rates are about 25-fold higher in ornithogenic versus mineral soils, reflecting organic C input by fecal material. A corresponding relationship exists between xylanase activity and TOC (Table 5). The high specific xylanase activity in the center of the penguin rookery at transect A can also be attributed to the input of organic C compounds by excrements. At transect B, specific xylanase activity responds to the TOC distribution (Fig. 6). As xylanase production is widely reported for fungi (Fenice et al., 1997), the low activity levels in the mineral soils may reflect the minor contribution of fungi to the microbial community. In contrast, Rustemeier (2001) reports 2- to 3-fold higher activity rates at comparable sites in the Alps. Bacteria, algae, and cyanobacteria are the most abundant organisms in antarctic soils (Bölter, 1992; Roser et al., 1993). Thus, the low numbers of fungi might be caused by the inhibitory effect of antifungal agents produced by bacteria (Czekanowska and Zabawski, 1988; Pietr, 1995).

Our data suggest that penguin guano and bird excrement enhance the amount of enzymes in the soil. Activities of the mineral soil are 1 (urease, xylanase) and 2 orders of magnitude (phosphatase, arylsulfatase) lower than those normally found in topsoils of temperate regions (Kandeler et al., 1996; Ajwa et al., 1999; Klose et al., 1999; Senwo and Tabatabai, 1999). The input of organic material by vegetation and birds raises enzyme activities (urease, phosphatase and xylanase) to levels of those in temperate soils (Kandeler and Eder, 1993; Beyer et al., 1999b; Kandeler et al., 1999b). The very high biomass-based specific enzyme activities of urease and phosphatase indicate that ornithogenic soils from presently occupied penguin rookeries exhibit high levels of enzyme activities; this is probably not only soil microbially derived, but also from enzymes in faecal material. Pietr et al. (1983) and Speir and Ross (1994) have reported similar patterns for protease and acid phosphatase, strengthening the hypothesis that mineralization of organic compounds in the soil is supported by activities of enzymes derived from penguin intestines.

Conclusions and Perspectives for Future Research

This study is the first to report soil microbial biomass and enzyme activities in combination with soil ecological parameters in the terrestrial ecosystem of maritime Antarctica. Because of the fairly weak pedogenesis with respect to humus accumulation and nutrient release from chemical weathering, the level of most microbiological indicators is extremely low, except in the ornithogenic soils. The multivariate approach of discriminant analysis, based on nine microbiological variables, is a powerful tool in identifying the ornithogenic impact on antarctic soils. The present study also suggests that P levels above 1000 mg kg^{-1} inhibit microbial growth in maritime Antarctica. In temperate climates the qCO_2 has been used as an indicator of soil disturbance or stress impact. Little, however, is known about its suitability in cold climate regions. We conclude that the impact of penguin guano varies with soil microbial properties. Microbial biomass, respiration, and N-mineralization are stimulated by organic matter input along transect B, whereas high P-inputs at transect A restricted microbial growth. We show that enzymes are present in antarctic soils, and that high levels of biomass-based specific enzyme activity in the ornithogenic versus mineral soils result from continuous input of large quantities of enzyme-rich guano excreta. The potential stabilization processes of these enzymes and their interactions with environmental factors (e.g., water, TOC, acidity, phosphorus) should be determined in order to gain a better understanding of enzyme-related processes in ornithogenic soils.

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References Cited

Ajwa, H. A., Dell, C. J., and Rice, C. W., 1999: Changes in enzyme activities and microbial biomass of tallgrass prairie soil as related to burning and nitrogen fertilization. *Soil Biology and Biochemistry,* 31: 769–777.

Amato, M., and Ladd, J. N., 1988: Assay for microbial biomass based on ninhydrin-reactive nitrogen in extracts of fumigated soils. *Soil Biology and Biochemistry,* 20: 107–114.

Beyer, L., Bockheim, J., Campbell, I. B., and Claridge, G. G. C., 1999a: Properties, genesis and global significance of Antarctic Cryosols. *Antarctic Science,* 11: 387–398.

Beyer, L., Sieling, K., and Pingpank, K., 1999b: The impact of a low humus level in arable soils on microbial properties, soil organic matter quality and crop yield. *Biology and Fertility of Soils,* 28: 156–161.

Blume, H. P., Beyer, L., Bölter, M., Erlenheuser, H., Kalk, E., Kneesch, K., Pfisterer, U., and Schneider, D., 1997: Pedogenic zonation in soils of Southern circumpolar region. *Advances in GeoEcology,* 30: 69–90.

Blume, H. P., Beyer, L., Kalk, E., and Kuhn, D., 2002: Weathering and Soil Formation. *In* Beyer, L., and Bölter, M. (ed.), *Geoecology of Antarctic Ice-Free Coastal Landscapes. Ecological Studies 154.* Berlin: Springer Verlag, 115–138.

Bölter, M., 1992: Environmental conditions and microbiological properties from soils and lichens from Antarctica (Casey Station, Wilkes Land). *Polar Biology,* 11: 591–599.

Bölter, M., 1993: Effects of carbohydrates and leucine on growth of bacteria from Antarctic soils (Casey Station, Wilkes Land). *Polar Biology,* 13: 297–306.

Bölter, M., 1995: Distribution of bacterial numbers and biomass in soils and on plants from King George Island (Arctowski Station, Maritime Antarctica). *Polar Biology,* 15: 115–124.

Bölter, M., Blume, H. P., and Kappen, L., 1995: Bodenbiologische Untersuchungen in der maritimen und kontinentalen Antarktis (King George Island und Windmill Islands). 1. Umweltparameter und anorganische Nährstoffe. *Polarforschung,* 65: 41–61.

Bölter, M., Blume, H. P., Schneider, D., and Beyer, L., 1997: Soil properties and distributions of invertebrates and bacteria from King George Island (Artowski Station), maritime Antarctica. *Polar Biology,* 18: 295–304.

Campbell, I. B., and Claridge, G. G. C., 1987: *Antarctica: Soils, Weathering Processes and Environment.* Amsterdam: Elsevier Publisher. 368 pp.

Christie, P., 1987: Nitrogen in two contrasting Antarctic bryophyte communities. *Journal of Ecology,* 75: 73–93.

Czekanowska, E., and Zabawski, J., 1988: Soil actinomycetes of the Admiralty Bay area at King George Island, Antarctic. *In* Jahn, A., Pereyma, J., and Szczepankiewicz-Szmyrka, A. (eds.), *XVth Polar Symposium: Present State and Selected Problems of Polish Polar Studies.* Wroctaw: Wroctaw Univ. Publ. House, 279–288.

Dixon, M., and Webb, E. C., 1979: *Enzymes.* 3rd ed. London: Longman Group. 54 pp.

FAO, 1990: *Guidelines for Soil Description.* 3rd ed. Rome: FAO.

Fenice, M., Selbmann, L., Zucconi, L., and Onofri, S., 1997: Production of extracellular enzymes by Antarctic fungal strains. *Polar Biology,* 17: 275–280.

Hoffmann, G., 1968: Eine photometrische Methode zur Bestimmung der Phosphataseaktivität in Böden. *Zeitschrift für Pflanzenernährung und Bodenkunde,* 118: 161–172.

Insam, H., and Haselwandter, K., 1989: Metabolic coefficient of the soil microflora in relation to plant succession. *Oecologia,* 79: 174–178.

Insam, H., and Öhlinger, R., 1995: Ecophysiological Parameters. *In* Schinner, F., Öhlinger, R., Kandeler, E., and Margesin, R. (eds.), *Methods in Soil Biology.* Berlin: Springer Verlag, 306–309.

Isermeyer, H., 1952: Eine einfache Methode zur Bestimmung der Bodenatmung und der Carbonate im Boden. *Zeitschrift für Pflanzenernährung und Bodenkunde,* 56: 26–38.

ISSS-FAO, 1998: World Reference Base for Soil Resources. FAO, ISRIC and ISSS. *World Soil Resource Report,* 84: 1–88.

Jäggi, W., 1976: Die Bestimmung der CO_2-Bildung als Mass der bodenbiologischen Aktivität. *Schweizer Landwirtschaftliche Forschung,* 15: 371–380.

Jenkinson, D. S., Hart, P. B. S., Rayner, J. H., and Parry, L. C., 1987: Modelling the turnover of organic matter in long-term experiments at Tothamsted. INTECOL-*Bulletin,* 15: 1–8.

Kaiser, E. A., Mueller, T., Joergensen, R. G., Insam, H., and Heinemeyer, O., 1992: Evaluation of methods to estimate the soil microbial biomass estimations and the relationship with soil texture and organic matter. *Soil Biology and Biochemistry,* 24: 675–683.

Kandeler, E., 1996: N-mineralization under waterlogged conditions. *In* Schinner, F., Öhlinger, R., Kandeler, E., and Margesin, R. (eds.), *Methods in Soil Biology.* Berlin: Springer Verlag, 141–143.

Kandeler, E., and Gerber, H., 1988: Short-term assay of soil urease activity using colorimetric determination of ammonium. *Biology and Fertility of Soils,* 6: 68–72.

Kandeler, E., and Eder, G., 1993: Effect of cattle slurry in grassland on microbial biomass and on activities of various enzymes. *Biology and Fertility of Soils,* 16: 249–254.

Kandeler, E., and Murer, E., 1993: Aggregate stability and soil microbial processes in a soil with different cultivation. *Geoderma,* 56: 503–513.

Kandeler, E., Eder, G., and Sobotik, M., 1994: Microbial biomass, N-mineralization, and the activities of various enzymes in relation to nitrate leaching and root distribution in a slurry-amended grassland. *Biology and Fertility of Soils,* 18: 7–12.

Kandeler, E., Kampichler, C., and Horak, O., 1996: Influence of heavy metals on the functional diversity of soil microbial communities. *Biology and Fertility of Soils,* 23: 299–306.

Kandeler, E., Kampichler, C., Joergensen, R. G., and Mölter, K., 1999a: Effects of mesofauna in a spruce forest on soil microbial communities and N cycling in field mesocosms. *Soil Biology and Biochemistry,* 31: 1783–1792.

Kandeler, E., Tscherko, D., and Spiegel, H., 1999b: Long-term monitoring of microbial biomass, N-mineralisation and enzyme activities of a Chernozem under different tillage management. *Biology and Fertility of Soils,* 28: 343–351.

Keeney, D. R., 1982: Nitrogen-availability indices. *In* Page, A. L., Miller, R. H., and Keeney, D. R. (eds.), *Methods of Soil Analysis*. Part 2. Madison, Wisc.: American Society of Agronomy, Soil Science Society America, 711–733.

Kenja, M., 1999: Air temperature on King George Island, South Shetland Islands, Antarctica. *Polish Polar Research,* 20: 183–201.

Kiss, M., Dragan-Bularda, M., and Radulescu, D., 1978: Soil Polysaccharidases: Activity and Agricultural Importance. *In* Burns, R. G. (ed.), *Soil Enzymes.* London: Academic Press, 117–140.

Klose, S., Moore, J. M., and Tabatabei, M. A., 1999: Arylsulfatase activity of microbial biomass in soils as affected by cropping systems. *Biology and Fertility of Soils,* 29: 46–54.

Kuhn, D., 1997: Genese, Ökologie und Soziologie einer Bodengesellschaft in einem Periglazialgebiet der King-George-In-

sel (West-Antarktis). *Schriftenreihe Institut für Pflanzenernährung und Bodenkunde Universität Kiel,* 40: 1–173.
Myrcha, A., and Tatur, A., 1991: Ecological role of the current and abandoned penguin rookeries in the land environment of the Maritime Antarctic. *Polish Polar Research,* 12: 3–24.
Öhlinger, R., 1993: Mikrobiologische Aktivität. *In* Amt der oberösterreichischen Landesregierung (ed.), *Oberösterreichische Bodenzustandsinventur 1993.* Linz: Landesverlag, 241–259.
Ohtonen, R., Fritze, H., Pennanen, T., Jumpponen, A., and Trappe, J., 1999: Ecosystem properties and microbial community changes in primary succession on a glacier forefront. *Oecologia,* 119: 239–246.
Olech, M. A., 1993: Lower Plants. *In* Rakusa-Suszczewski, S. (ed.), *The Maritime Antarctic Ecosystems of Admiralty Bay.* Warsawa, Department of Antarctic Biology, Polish Academy of Sciences: 173–179.
Olech, M. A., 2002: Plant Communities on King George Island. *In* Beyer, L. and Bölter, M. (eds.), *Geoecology of Antarctic Ice-Free Coastal Landscapes. Ecological Studies 154.* Berlin: Springer Verlag, 215–231.
Orchard, M. A., and Corderoy, D. M., 1983: Influence of environmental factors on the decomposition of penguin guano in Antarctica. *Polar Biology,* 1: 199–204.
Pietr, S. J., 1995: Soil Microorganisms. *In* Rakusa-Suszczewski, S. (ed.), *The Maritime Antarctic Ecosystems of Admirality Bay*. Warsawa: Department of Antarctic Biology, Polish Academy of Sciences, 167–172.
Pietr, S. J., Tatur, A., and Myrcha, A., 1983: Mineralization of penguin excrements in the Admiralty Bay region (King George Island, South Shetland Islands, Antarctica). *Polish Polar Research,* 4: 97–112.
Rakusa-Suszczewski, S., 2002: King George Island—South Shetland Islands, Maritime Antarctic. *In* Beyer, L., and Bölter, M. (eds.), *Geoecology of Antarctic Ice-Free Coastal Landscapes. Ecological Studies 154.* Berlin: Springer Verlag, 23–39.
Rakusa-Suszczewski, S., Mietus, S., and Piasecki, J., 1993: Weather and Climate. *In* Rakusa-Suszczewski, S. (ed.), *The Maritime Antarctic Ecosystems of Admiralty Bay.* Warsaw: Department of Antarctic Biology, Polish Academy of Sciences, 19–25.
Ramsay, A. J., and Stannard, R. E., 1986: Numbers and viability of bacteria in ornithogenic soils of Antarctica. *Polar Biology,* 5: 195–198.
Ray, M. K., Shivaji, S., Shyamala Rao, N., and Bhargava, P. M., 1989: Yeast strains from the Schirmacher Oasis, Antarctica. *Polar Biology,* 9: 305–309.
Roser, D. J., Seppelt, D. R., and Ashbolt, N., 1993: Microbiology of ornithogenic soils from the Windmill Islands, Budd Coast, continental Antarctica: microbial biomass distribution. *Soil Biology and Biochemistry,* 25: 165–175.
Rustemeier, J., 2001: *Bodenmikrobiologische Eigenschaften entlang einer Chronosequenz zweier Gletschervorfelder in den österreichischen Alpen.* Thesis. Osnabrück: University of Applied Sciences. 148 pp.
Schinner, F., and von Mersi, M., 1990: Xylanase-, CM-cellulase- and invertase activity in soil: an improved method. *Soil Biology and Biochemistry,* 22: 11–515.
Schlichting, E., Blume, H. P., and Stahr, K., 1995: *Bodenkundliches Praktikum.* Berlin: Blackwell, 295 pp.
Senwo, Z. N., and Tabatabai, M. A., 1999: Aspartase activity in soils: effects of trace elements and relationships to other amidohydrolases. *Soil Biology and Biochemistry,* 31: 213–219.
Speir, T. W., and Ross, D. J., 1978: Soil Phosphatase and Sulphatase. *In* Burns, R. G. (ed.), *Soil Enzymes*. London: Academic Press, 198–235.
Speir, T. W., and Ross, D. J., 1984: Ornithogenic soils of the Cape Bird Adelie Penguin Rookeries, Antarctica. 2. Ammonia evolution and enzyme activities. *Polar Biology,* 2: 207–212.
Tabatabai, M. A., and Bremner, J. M., 1969: Use of p-nitrophenylphosphate for assay of soil phosphatase activity. *Soil Biology and Biochemistry,* 1: 301–307.
Tabatabai, M. A., and Bremner, J. M., 1970: Arylsulfatase activity of soils. *Soil Science Society of America Journal,* 34: 225–229.
Tatur, A., and Myrcha, A., 1984: Ornithogenic soils on King George Island, South Shetland Islands (Maritime Antarctic Zone). *Polish Polar Research,* 5: 31–60.
Tearle, P. V., 1987: Cryptogamic carbohydrate release and microbial response during spring freeze-thaw cycles in antarctic fellfield fines. *Soil Biology and Biochemistry,* 19: 381–390.
Tibbles, B. J., and Harris, J. M., 1996: Use of radiolabelled thymidine and leucine to estimate bacterial production in soils from continental Antarctica. *Applied and Environmental Microbiology,* 62: 694–701.
UNOG, 2000: The Antarctic Treaty and the Protocol on the Environmental Protection to the Antarctic Treaty. http://www.unog.ch/disarm/distreat/antarc.htm
von Mersi, W., Kuhnert-Finkernagel R., and Schinner, F., 1992: The influence of rock powders on microbial activity of three forest soils. *Zeitschrift für Pflanzenernährung und Bodenkunde,* 155: 29–33.
Wynn-Williams, D. D., 1982: Simulation of seasonal changes in microbial activity of maritime antarctic peat. *Soil Biology and Biochemistry,* 14: 1–12.
Zarzycki, K., 1993: Vascular plants and terrestrial biotopes. *In* Rakusa-Suszczewski, S. (ed.), *The Maritime Antarctic Coastal Ecosystem of Admiralty Bay*. Warsaw: Department of Antarctic Biology, Polish Academy of Sciences, 181–187.
Zechmeister-Boltenstern, S., Spadinger, K., and Kinzel, H., 1991: Bodenenzymatische Untersuchungen in verschieden stark belasteten Buchenwaldstandorten. *In* Albert, R., Burian, K., and Kinzel, H. (eds.), *Zustandserhebung Wienerwald. Pflanzenphysiologische und bodenökologische Untersuchungen zur Bioindikation.* Vienna: Verlag der Österreichischen Akademie der Wissenschaften.

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