Variation in the characteristics and development of soils at Edmonson Point due to abiotic and biotic factors, northern Victoria Land, Antarctica

Jerzy Smykla, Marek Drewnik, Ewa Szarek-Gwiazda, Yii Siang Hii, Wiesław Knap, Steven D. Emslie

1. Introduction

Terrestrial, ice-free environments in Antarctica are restricted to only ~0.34% of the entire Antarctic continent, equating to ~45 000 km², with the reminder permanently covered by glaciers and snow (Convey et al., 2009b). Most of these ice-free environments occur as isolated patches of ground scattered along the continental coasts and relatively few are found inland. These locations are characterized by frigid climate with very low temperatures, humidity and precipitation and strong katabatic winds. Due to such extreme climatic conditions, Antarctic terrestrial environments are some of the harshest on Earth. Moreover, many of the Antarctic ice-free areas have emerged from retreating glaciers during the past few thousand years and glacial erosion is still the dominant land-forming factor. Therefore, the ground is mostly barren of any visible vegetation and is primarily covered with glacier till, unsorted rock rubble, gravel and scattered erratic boulders (Campbell and Claridge, 1987; Beyer and Bölter, 2002).

As a consequence of the extreme climatic conditions and relatively short exposure in most of the Antarctic ice-free areas, the soils are weakly developed and lack cohesion and structural development.
Moreover, in specific conditions pedological processes might be restricted to endolithic environments (Mergelov et al., 2012). Consequently, until recently many scientists were unwilling to identify them as soils. In fact, in many of the Antarctic ice-free areas, the existence of soil in a strict sense is still disputed. Given their very limited and widely scattered distribution, poor development and lack of suitability for any potential land use, Antarctic soils were considered of minor importance and received relatively little attention by soil scientists. Therefore the study of Antarctic soils is comparatively new, but their significance is drawing more attention, particularly with respect to environmental and ecosystem relationships (Beyer and Böltter, 2002; Kimble, 2004; Wall, 2005; Ugolini and Bockheim, 2008).

Because of their extreme environmental conditions, Antarctic soils are regarded as sensitive indicators of environmental changes and human impacts (Wall, 2005; Ugolini and Bockheim, 2008). The three most important physical factors in context with climate change for Antarctic terrestrial habitats are temperature, water availability and solar irradiance (Kennedy, 1995; Convey and Lewis Smith, 2006). Rapid changes in all three of these major environmental variables have been documented in the Antarctic, particularly in the maritime region (Kennedy, 1995; Turner et al., 2014). Although there is no evidence of rapid climate change on the Antarctic continent, its terrestrial ecosystems are climatically very sensitive (Ugolini and Bockheim, 2008) and it is widely expected that current global climate changes are likely to have major impacts on the ice-free environments (Kennedy, 1995; Wall, 2005; Convey et al., 2009a; Turner et al., 2014).

Soils also provide information on environmental changes in Antarctica as they record variation in past and present conditions (Navas et al., 2008; Liu et al., 2013; Nie et al., 2014). Antarctic soils could, therefore, be one of the more significant baseline environments for the study of global climate changes. This application using soils and the biota they support to assess impacts of climate change necessitate a full understanding of Antarctic soil processes and geochemistry (Beyer and Böltter, 2002; Wall, 2005; Barrett et al., 2006a, 2006b). Previous research on Antarctic soils, their properties and biotic communities, however, has focused mostly on those in the McMurdo Dry Valleys and relatively little is known about them at other localities (Beyer and Böltter, 2002; Kimble, 2004; Ugolini and Bockheim, 2008). Only a few studies were conducted at other Victoria Land localities (e.g. Cannone et al., 2008; Cannone and Guglielmin, 2009), at Wilkes and Dronning Maund Lands and on soils of the maritime Antarctic (see Everett, 1976; Beyer and Böltter, 2002; Böltter, 2011). The relationship among soils, the landscape and the glacial history were the focus for most of these studies (Ugolini and Bockheim, 2008).

Numerous studies also have focused on ornithogenic soils formed within penguin colonies (see recent review by Emslie et al., 2014). Ornithogenic soils have been especially studied on King George Island in the maritime Antarctic (Tatur and Myrcha, 1984; Tatur, 1989, 2002; Myrcha and Tatur, 1991; Michel et al., 2006), but also at a few locations around the Antarctic continent, particularly in the Ross Sea region, i.e. on Ross Island (Ugolini, 1972; Speir and Cowling, 1984; Speir and Ross, 1984; Heine and Speir, 1989), Inexpressible Island (Campbell and Claridge, 1966) and Cape Hallet (Hofstee et al., 2006). These studies concentrated primarily on the ornithogenic soil physical and chemical properties, but some also investigated influences of soil ornithogenic compounds on abundance and distribution patterns of soil biota (Ramsay, 1983; Ramsay and Stannard, 1986; Roser et al., 1993; Porazinska et al., 2002; Smykla et al., 2010, 2012) or vegetation (Tatur et al., 1997; Michel et al., 2006; Smykla et al., 2007; Krywult et al., 2013).

The lack of baseline surveys of Antarctic soils, as highlighted above, provides a serious impediment to understanding their suitability for supporting biotic communities, and it also limits our abilities to monitor and predict the impact of current environmental changes in Antarctic terrestrial ecosystems. To increase the existing knowledge on biogeochemistry of Antarctic soils, we have investigated and sampled several localities in the Ross Sea area (see Smykla et al., 2011). Initially, this work focused on active and relict penguin colonies and influences of these colonies on soil geochemistry and biotic communities. Ultimately, the work was extended to include other soil environments near our surveyed localities to provide background references to the ornithogenic soils.

Here, we present the analysis of the key physical, chemical and biogeochemical characteristics of soils at Edmonson Point, Victoria Land, Ross Sea (Figs. 1–2a). Soils in the Edmonson Point area have previously been investigated, but this research focused mostly on the bryophyte communities or lacustrine environments (Bargagli et al., 1998, 1999; Lewis Smith, 1999; Cannone et al., 2008; Cannone and Guglielmin, 2009; Malandrino et al., 2009). Previous investigations have indicated the presence of an exceptionally wide range of terrestrial environments with high abundance of water and rich biotic communities (Harris and Grant, 2003). Thus, Edmonson Point is a useful model site for understanding processes and changes of coastal ice-free ecosystems in this region. During our investigations we included a more representative examination of various soil environments and provide a comprehensive analysis of soil characteristics in this area. We sought to identify soil variability and define the main drivers of soil processes and geochemistry. We hypothesized that the soil, despite being geologically young with similarities to the parent material, will show significant variation in its characteristics across local environments, with differences driven by hydrology and associated biological processes. External inputs, related to the presence of penguin colonies, were also expected to have pronounced effects on soil development and geochemical cycling in this area.

2. Material and methods

2.1. Description of study area

Edmonson Point (74°20′S, 165°08′E) is located in Wood Bay on the west coast of the Ross Sea, northern Victoria Land, Continental Antarctica (Figs. 1–2a). It is an ice-free coastal spur of Mount Melbourne, a dormant volcano showing evidence of very recent activity (Kyle, 1990). The area encompasses ~6 km² and is one of the largest non-mountainous, coastal ice-free areas in northern Victoria Land. The landscape of Edmonson Point has been considerably modified by glacial and periglacial activity, resulting in a mosaic of hills (up to 300 m high), knolls and moraines, separated by small valleys with several ephemeral melt-water streams, seepage areas, ponds and a few larger lakes. Such a range of freshwater environments in one area is unusual and the stream network is the most extensive for the whole of Victoria Land. Most of the area, however, is extremely dry with the ground covered by salt crustations (Fig. 2a–b). The ground is dark colored and consists of volcanic materials (basaltic lavas, scoria, pumice and tuff) which originated from the past volcanic activity of Mount Melbourne. Only in a relatively narrow strip of modern and raised beaches are the parent materials reworked by marine processes and consist also of some marine deposits (Baroni and Orombelli, 1994). The climate is typical of coastal areas in the continental Antarctic, with low temperature, humidity and precipitation. However, the area of Edmonson Point is well sheltered from local katabatic winds, and its climate is milder than in the neighboring areas, with the temperature during the austral summer ranging from −11° to +12 °C and is above freezing every day for about 6–10 weeks (Harris and Grant, 2003, Cannone and Guglielmin, 2009).

As in most of the Antarctic ice-free terrestrial ecosystems low temperatures and aridity are the main limiting factors for life at Edmonson Point. However, owing to a relatively mild climate, availability of liquid water and bird-derived nutrients, Edmonson Point compared with other sites in Victoria Land has a wide range of terrestrial environments and a relatively diverse biota. Flora of this area is entirely cryptogamic, with bryophytes (six mosses, one liverwort) and lichens (~30 species) being the principal composition of plant communities. Although it seems very poor in species, Edmonson Point possesses exceptionally...
extensive bryophyte vegetation with the most extensive contiguous moss carpets known in Victoria Land (Lewis Smith, 1999; Harris and Grant, 2003). On the other hand, communities of lichens are not as well-developed compared with some other ice-free sites in Victoria Land (Castello, 2003; Smykla et al., 2011). Reflecting on the wide range of freshwater environments, the diversity of algae seems to be the highest in Victoria Land with over 100 species recorded (Fumanti and Cavacini, 2005). Also, the diversity of soil mycobiota is exceptionally high and is related to the diversity of soil characteristics (Tosi et al., 2005). The terrestrial fauna is limited to soil invertebrates, such as springtails, mites, nematodes, tardigrades, rotifers and protozoans, which although not particularly diverse are especially abundant (Harris and Grant, 2003; Smykla et al., 2010, 2012). The avian community consists of the Adélie penguin (*Pygoscelis adeliae*), estimated at ~2000 breeding pairs, and the south polar skua (*Catharacta maccormicki*), with a population of about 100 pairs (Pezzo et al., 2001). Because of these outstanding ecological values, Edmonson Point is considered exceptional for research on biotic communities. Therefore, following an Italian proposal, Edmonson Point was designated as an Antarctic Specially Protected Area (ASPA) No. 165 in June 2006.

### 2.2. Field survey and soil sampling

During the Antarctic summers of 2003/04 and 2004/05, a field survey was conducted in the Edmonson Point area to identify and sample representative soil environments as part of an investigation on their characteristics, biogeochemistry and biota diversity. The locations selected for soil sampling represented a range of different arbitrarily defined environments with a diversity of physical and chemical characteristics of the soil, including (1) fellfields (i.e., dry and unvegetated areas), (2) moss communities, (3) wetlands (i.e., wet depressions covered with algal and cyanobacterial mats, supplied with water draining from the melting permafrost and/or snowmelt) as well as (4) active and (5) relict penguin colonies (Fig. 2b–f).

A total of 42 soil samples were collected from all investigated environments. The samples were collected from the upper soil layer (0–10 cm deep) using a sterile scoop, then placed into sterile polyethylene bags (Whirl-Pack®). To obtain homogeneous material for different analyses each sample was mixed thoroughly immediately after collecting and split into separate bags. Gravel larger than ~5 mm diameter was removed from the samples in the field. The soil sampling depth was chosen to correspond with previous investigations on soil biota diversity (Courtright et al., 2001; Porazinska et al., 2002; Barrett et al., 2004, 2006b; Bamforth et al., 2005). This approach was also adopted to accommodate limited time in the field due to logistic constraints. While collecting only surface soils could limit conclusions about soil development processes and geochemistry due to strong cryoturbation and very weak pedogenesis of Antarctic soils, there are typically no pronounced differences between surface and subsurface soils. The lack of developed soil profiles is particularly visible in geologically young soils in ice-free coastal sites (Campbell and Claridge, 1987). Quantities sampled were limited to achieve the best possible compromise between avoiding disturbance of the surface and still obtaining enough soil for adequate analyses. In moss communities the samples were collected...
directly at and/or among moss cushions, but to limit disturbances mosses were not removed from the sampling sites.

Within a few hours after collection, all samples were transported to the Italian Station Mario Zucchelli at Terra Nova Bay and frozen by reducing the temperature over 48-h period from 1° to −20 °C. The samples were shipped in a frozen state to the Institute of Nature Conservation, Polish Academy of Sciences, for processing and analyses.

2.3. Laboratory analyses

In the lab samples were thawed over a 24-h period from −20 °C to 3 °C and analyzed for the following physical, chemical and biological parameters: soil texture, moisture, pH, salinity, elemental composition including C, N, P, Ca, K, Mg and Na, bacteria numbers and concentration of algal assimilation pigments. A broad range of standard analytical methods commonly used in soil science was applied to provide detailed characterization of the soils.

Soil texture was evaluated by dry sieving for coarse (>2 mm) and sand fractions (0.05–2 mm), and using a laser diffraction analysis (LDA) for clay and silt fractions (<0.05 mm). The LDA analysis was done using the device Analysette 22, Fritsch. To eliminate the organic matter, prior to the LDA analysis samples were chemically disaggregated with 10% H2O2 heated to 80 °C, then stirred and an ultrasound was also used to facilitate particle dispersion. The proportion of coarse fraction (>2 mm) was calculated based upon its weight as a percentage of the total sample weight. The proportions of sand (0.05–2 mm), silt (0.002–0.05 mm) and clay (>0.002) were calculated as a percentage of a particular fraction in the sample fine-soil fraction (<2 mm). Soil texture classification followed USDA Soil Taxonomy.

Soil moisture was determined gravimetrically based upon weight loss from fresh (field-moist) samples dried in an oven at 105 °C for 24 h, and calculated as the percentage per dry weight of the fine-soil fraction (<2 mm). Soil pH was measured on a 1:2.5 (w/v) soil:deionized water slurry (8 g soil:20 ml water). Salinity was estimated by measuring the electrical conductivity (EC) in a 1:5 (w/v) soil:deionized water mixture (4 g soil:20 ml water). The measurements were completed at room temperature using Elmetron multifunctional meter CX-742 equipped with pH electrode WTW Sentix 62, conductivity meter Hydromet CDT-3 or CDT-2 (for values above 10 dS m−1) and an automatic temperature correcting probe.

Total C and N contents were determined by the dry combustion gas chromatography with a CHN analyzer (Thermo Finnigan EA 1112). Approximately 2.5–3.0 mg of dry sample (<500 μm) was weighed in ultrapure tin combustion capsules, placed into the analyzer and burned in a pure oxygen environment (99.996%). The combustion gases were then passed by a stream of Helium gas over the spectral columns and the components were measured by the thermal conductivity detector (TCD). The C and N contents were calculated based on the sample peak area and a standard calibration curve obtained using different weights of ultra-high purity acetonilide [C9H5NH(COCH3)] ranging

![Fig. 2. General view of the study area and investigated environments: a) aerial view of the southern part of the Edmonson Point area, b) bare fellfields (BFs) showing the most common soil parent material in the study area with salt encrustations (top of the picture), c) moss communities (MCs), d) wetland soils (WETs) colonized by microbial/algal mats (picture shows a site of a decomposition experiment), e) active penguin colony (APC), and f) soil profile at a relict penguin colony (RPC).](image-url)
from 0.1 to 0.8 mg. Empty tin-capsule blanks were also included into each batch of samples to obtain a true zero baseline.

Determination of the total P, Ca, K, Mg and Na contents was performed through Inductivity Coupled Plasma Mass Spectrometry (ICP-MS, Elan 6100, Perkin Elmer). Prior to the analysis approximately 0.5 g of each dry sample was digested with a mixture of nitric (HNO₃) and hydrochloric (HCl) acids (4:1) using microwave Speed Wave, Berghof. The accuracy and precision of the analytical procedures were verified through analysis of blanks and determination of elemental concentrations in standard reference material (NCS DC 73308).

Available P was determined by the modified extraction method of Bray 2 (Olsen and Sommers, 1982) followed by spectrophotometry. Briefly, 20 ml of water was added to 2–5 g of soil sample (~500 µm) and agitated at 150 rpm for 1 h. The solution was then centrifuged at 6000 rpm for 10 min, then filtered and acidity to pH 2 by adding 1 ml of 6 M HCl to prevent precipitation of phosphorus compounds. Then 5.0 ml of the sample solution was mixed with 0.5 ml of a reagent (75 ml 4% (v/v) ammonium molybdate solution, 250 ml 5 N HCl, 150 ml 0.01 M ascorbic acid and 25 ml 0.004 M potassium antimonyl tartate solution) and then left to react for 1 h. The absorbance of the sample was measured colorimetrically at 520 nm using a double beam UV–VIS spectrophotometer (Shimadzu UV1800). Concentration of the available P was calculated on the basis of a calibration curve for Potassius dihydrogen phosphate [KH₂PO₄] (0–1.0 mg l⁻¹). A distilled water blank and a spiked standard (1.0 mg/g) were analyzed together with the sample.

The total number of bacterial cells was determined following the epifluorescent DAPI staining method (Bloem et al., 1992). Approximately 2.5 g of fresh soil was homogenized in 90 ml of sterile filtered water by ultrasonication for 3 min followed by mixing on a vortex for 1 min. The mixtures were left to settle coarse soil particles for 1 min. Then, 1.8 ml of the soil solution was fixed with 0.2 ml of methanol (37%) and further serially diluted 10⁻³–10⁻⁶ in sterile water (final diluted solution represented ca. 2.5–250 µg fresh soil ml⁻¹). Diluted soil extracts (1 ml) were put on a 0.2 µm black Nucleopore filter (Poretics Products, Osmonics) and stained with DAPI (50 µl, 100 mg ml⁻¹ solution) for 2 min. Then 2 ml of sterile water was added and filtered using a vacuum pump. Bacteria were counted immediately after staining and filtering. All bacteria within 40 squares of the eyepiece graticule were counted (ca. 300–2000 bacterial cells per sample). Samples were observed under oil immersion with an Olympus BX 61 epifluorescence microscope, equipped with a UVA-2A Ex 330–380 filter, 100 W mercury lamp and U Plan APO 100x 1.4 objective.

The concentrations of algal assimilation pigments were determined with a spectrophotometer using a modified method of Kirkwood and Henley (2006). Approximately 5 ml of fresh soil sample was mixed well with N,N-dimethylformamide (DMF) in a 1:1 (v/v) ratio, vortexed at 2200 rpm for 1 min and left to extract in dark at room temperature overnight. The supernatant was then centrifuged at 3000 g at 4 °C for 5 min to clarify it. Pigment concentrations were determined by scanning absorbance at 400–750 nm using the UV-1650PC spectrophotometer (Shimadzu, Japan). For calculations, absorbance at 750, 664, 647, 630, 510 and 480 nm were used. Chlorophyll a, b, c₁, c₂ and bulk carotenoid values were corrected by subtracting absorbance measured at A750 and then calculated using the formulas of Jeffrey and Humphrey (1975).

2.4. Statistical analyses

Mean values and standard deviation (SD) of all the assessed parameters for all different soil environments were calculated. Differences among investigated soil environments in all measured physico-chemical and biological parameters were tested using one-way ANOVA. Tukey Honestly Significant Differences (HSDs) were calculated to determine post-hoc pair-wise comparisons among environment means from the significant (α = 0.05) ANOVA tests. Matrix of Pearson’s correlation coefficients (r) was calculated to detect pair-wise relationships among the different soil characteristics. ANOVA and Pearson’s correlation coefficients were computed with the software package STATISTICA 10.0 (StatSoft Inc, Tulsa, OK, USA).

3. Results

Descriptive statistics, calculated for the investigated soil characteristics as a function of the environment, are presented in Table 1. The data demonstrate that the soil characteristics varied significantly among the investigated environments, but they were also highly variable within particular environments. The data also indicate that the most significant differences among the investigated environments are related to past and present activity of penguins, i.e. the presence of relict and active penguin colonies; thus, the investigated soils can be divided into two very distinct groups: (1) mineral soils comprised of gravel and sand, dominated by weakly weathered basalts and (2) ornithogenic soils that developed due to the long lasting addition of penguin guano.

3.1. Soil physical and chemical characteristics

The investigated soils were coarse-textured, lacking in cohesion and structural development. They consisted of a high amount of gravel and rock and had a very low proportion of silt and clay. The amount of coarse fraction (≥ 2 mm) was highest at fellfields and penguin colonies relative to soils from moss communities and wetlands (ANOVA, F = 5.68, P = 0.001). The contents of the soil fine fractions (< 2 mm) were dominated by sand, with mostly coarse sandy soils (35 samples) or medium sandy (two samples), loamy coarse sandy (two samples) and loamy medium sandy sands (two samples). Only one sample from a relict penguin colony showed a silty loamy texture and was characterized by very high silt and clay content (60.6%). Because of very low amount of clay, which in most cases was lower than 1%, for further analyses silt and clay fractions were pooled. While the amount of sand was the highest at fellfields, moss communities and active penguin colonies, the content of silt and clay fractions was the highest in wetlands and relict penguin colonies (F = 3.81, P = 0.001).

Soil moisture was highly variable among different environments (F = 9.08, P = 0.0004), which can be arranged into a hydrological gradient, with the lowest values in fellfields (6.2–26.4%), intermediate in moss communities (24.1–159.0%) and the highest in wetland soils (60.9–210.7%). Soils from active (2.7–10.6%) and relict (4.1–28.8%) penguin colonies both had very low soil moisture content. The Pearson’s correlation matrix indicates a positive relationship of soil moisture with a majority of the investigated characteristics and negative relationship only with pH values, contents of gravel and total P (Table 2).

Soil pH ranged from slightly alkaline to very strongly acidic (4.9–7.6) and varied significantly among investigated environments (F = 4.49, P = 0.005). At fellfield pH was close to neutral ranging from slightly alkaline to slightly acidic (6.4–7.6). At wetlands and moss communities the pH was significantly lower ranging from neutral to moderately acidic at wetlands (6.0–6.7) and to very strongly acidic in moss communities (4.9–6.8). The pH of ornithogenic soils ranged from neutral to slightly acidic at active (6.1–7.0) and relict (6.4–6.9) penguin colonies. Electrical conductivity (EC) values spanned three orders of magnitude (0.08–17.69 dS m⁻¹). The lowest values were found in soils from fellfields (0.10–0.15 dS m⁻¹) and moss communities (0.08–0.24 dS m⁻¹), higher values were recorded in wetland soils (0.34–1.33 dS m⁻¹), whereas the highest values were found in soils from relict (1.85–4.30 dS m⁻¹) and active (2.41–17.70 dS m⁻¹) penguin colonies (F = 8.01, P = 0.0001).

Contents of the soil total C also varied significantly (F = 4.35, P = 0.02) from very low values found in soils from fellfields, intermediate in soils from moss communities and the highest in wetland soils. Ornithogenic soils also had very high C contents, with values within the same range as in wetland soils. Distribution of soil total N contents...
exhibited a very similar pattern. Its contents were the lowest at fellfields and progressively higher in moss communities and wetlands. The highest values were found in soils from active and relic penguin colonies (F = 7.10, P < 0.0003). The data also demonstrate lower values of both C and N in soils from relic colonies compared with those from active colonies. Although the differences were not statistically significant due to very high variability, they indicate loss of C and N in ornithogenic soils with time.

Concentrations of the total P and available P did not exhibit significant differences among mineral soils, but their contents in ornithogenic soils were markedly higher (F = 38.78 and F = 26.44, P < 0.0001, respectively). Ornithogenic soils were homogenous with respect to available P. Concentrations of the total P and available P did not exhibit significant differences among particular environments from the one-way ANOVA at P < 0.05.

Chlorophyll content also was highly variable and exhibited significant differences among investigated soil environments (Table 1), including total chlorophyll (F = 9.84, P = 0.00002) and all its major components: chlorophyll a (F = 13.31, P < 0.0001), chlorophyll b (F = 9.87, P = 0.00002) and chlorophyll c1 + c2 (F = 10.61, P = 0.0001). Only carotenoids, which had very low values, did not show statistical differences among the investigated soils (F = 0.45, P = 0.77). In general fellfield soils had the lowest amount of chlorophylls, followed by soils from moss communities and wetlands. This pattern mirrors that of the bacteria in demonstrating the importance of moisture for abundance of microflora in mineral soils. The Pearson’s correlations also indicated a positive relationship of chlorophylls with moisture, but also with C, N, available P and all bio-elements (i.e. Ca, K, Mg, Na) [Table 2]. Soils from active and relic penguin colonies with respect to chlorophyll contents were very homogeneous. Although moisture content of ornithogenic soils was low they had very high contents of the total chlorophyll, with values similar to wetland soils. Contents of particular types of chlorophylls, however, showed different patterns in relation to wetland soils, while the amount of chlorophyll a in ornithogenic soils was over two times lower than chlorophyll b and chlorophyll c1 + c2. This result indicates high differences among soil environments in taxonomic composition of the microflora. Significant differences in proportion of chlorophyll a/b (F = 4.72, P = 0.004) also indicate strong differences between ornithogenic compared to mineral soils in their biological characteristics.

Table 1

<table>
<thead>
<tr>
<th></th>
<th>BF (n = 6)</th>
<th>MC (n = 15)</th>
<th>WET (n = 11)</th>
<th>APC (n = 5)</th>
<th>RPC (n = 5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moisture</td>
<td>%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>6.82 ± 0.5</td>
<td>6.08 ± 0.57</td>
<td>6.28 ± 0.27</td>
<td>6.69 ± 0.22</td>
<td>6.68 ± 0.19</td>
</tr>
<tr>
<td>EC</td>
<td>0.11 ± 0.02</td>
<td>0.15 ± 0.04</td>
<td>0.70 ± 0.31</td>
<td>7.46 ± 6.52</td>
<td>3.31 ± 1.08</td>
</tr>
<tr>
<td>Gravel</td>
<td>27.2 ± 9.1</td>
<td>17.3 ± 9.2</td>
<td>15.9 ± 8.2</td>
<td>37.4 ± 4.2</td>
<td>30.3 ± 8.3</td>
</tr>
<tr>
<td>Sand</td>
<td>94.4 ± 6.7</td>
<td>94.3 ± 5.2</td>
<td>90.3 ± 3.4</td>
<td>97.6 ± 1.3</td>
<td>86.4 ± 6.5</td>
</tr>
<tr>
<td>Silt + clay</td>
<td>5.6 ± 6.7</td>
<td>5.7 ± 5.2</td>
<td>9.7 ± 3.4</td>
<td>2.3 ± 1.3</td>
<td>13.6 ± 6.5</td>
</tr>
<tr>
<td>C</td>
<td>mg g⁻¹</td>
<td>12.7 ± 2.69</td>
<td>23.70 ± 25.20</td>
<td>46.66 ± 32.45</td>
<td>42.55 ± 23.90</td>
</tr>
<tr>
<td>N</td>
<td>mg g⁻¹</td>
<td>0.16 ± 0.31</td>
<td>1.44 ± 2.05</td>
<td>4.00 ± 3.33</td>
<td>13.86 ± 9.30</td>
</tr>
<tr>
<td>P total</td>
<td>mg g⁻¹</td>
<td>0.873 ± 0.494</td>
<td>0.823 ± 0.428</td>
<td>0.732 ± 0.483</td>
<td>0.808 ± 5.470</td>
</tr>
<tr>
<td>P available</td>
<td>0.109 ± 0.086</td>
<td>0.100 ± 0.090</td>
<td>0.174 ± 0.112</td>
<td>0.474 ± 0.120</td>
<td>0.540 ± 0.083</td>
</tr>
<tr>
<td>C/N</td>
<td></td>
<td>6.15 ± 1.48</td>
<td>14.32 ± 7.57</td>
<td>12.25 ± 3.33</td>
<td>13.32 ± 0.58</td>
</tr>
<tr>
<td>C/P</td>
<td></td>
<td>0.13 ± 1.87</td>
<td>24.89 ± 36.16</td>
<td>69.56 ± 37.45</td>
<td>5.42 ± 6.70</td>
</tr>
<tr>
<td>N/P</td>
<td></td>
<td>0.11 ± 0.16</td>
<td>1.46 ± 1.91</td>
<td>6.17 ± 3.98</td>
<td>2.01 ± 2.82</td>
</tr>
<tr>
<td>Ca</td>
<td>mg g⁻¹</td>
<td>3,043.6 ± 628.9</td>
<td>2,856.4 ± 941.9</td>
<td>10,780.1 ± 4,320.5</td>
<td>11,479.8 ± 4,404.8</td>
</tr>
<tr>
<td>K</td>
<td>mg g⁻¹</td>
<td>805.5 ± 187.9</td>
<td>764.5 ± 252.8</td>
<td>1,674.7 ± 741.4</td>
<td>2,025.5 ± 1,630.3</td>
</tr>
<tr>
<td>Mg</td>
<td>mg g⁻¹</td>
<td>2,487.7 ± 172.2</td>
<td>2,297.4 ± 854.5</td>
<td>7,929.7 ± 3,836.6</td>
<td>10,040.2 ± 1,340.4</td>
</tr>
<tr>
<td>Na</td>
<td>mg g⁻¹</td>
<td>1,252.8 ± 262.5</td>
<td>1,507.9 ± 519.1</td>
<td>4,861.2 ± 2,370.1</td>
<td>5,085.4 ± 3,853.1</td>
</tr>
<tr>
<td>Chlorophyll total</td>
<td>mg ml⁻¹</td>
<td>3.46 ± 4.51</td>
<td>5.37 ± 3.51</td>
<td>17.26 ± 6.10</td>
<td>17.59 ± 14.03</td>
</tr>
<tr>
<td>Chlorophyll a</td>
<td>mg ml⁻¹</td>
<td>0.78 ± 1.51</td>
<td>1.51 ± 2.13</td>
<td>7.93 ± 3.18</td>
<td>3.90 ± 2.62</td>
</tr>
<tr>
<td>Chlorophyll b</td>
<td>mg ml⁻¹</td>
<td>0.27 ± 0.56</td>
<td>0.76 ± 0.70</td>
<td>2.18 ± 1.02</td>
<td>5.74 ± 5.24</td>
</tr>
<tr>
<td>Chlorophyll c₁ + c₂</td>
<td>mg ml⁻¹</td>
<td>0.15 ± 0.24</td>
<td>0.87 ± 0.66</td>
<td>3.33 ± 2.39</td>
<td>7.03 ± 6.45</td>
</tr>
<tr>
<td>Chlorophyll a/b</td>
<td></td>
<td>2.23 ± 3.57</td>
<td>2.02 ± 0.83</td>
<td>3.74 ± 0.87</td>
<td>0.78 ± 0.16</td>
</tr>
<tr>
<td>Carotenoids</td>
<td>mg ml⁻¹</td>
<td>0.02 ± 0.03</td>
<td>0.10 ± 0.11</td>
<td>0.08 ± 0.26</td>
<td>0.13 ± 0.25</td>
</tr>
<tr>
<td>Bacteria</td>
<td>x 10⁹ g⁻¹</td>
<td>0.19 ± 0.08</td>
<td>31.22 ± 22.82</td>
<td>31.63 ± 35.79</td>
<td>79.36 ± 60.24</td>
</tr>
</tbody>
</table>

3.2. Soil biological characteristics

Bacterial numbers ranged across three orders of magnitude (0.112 ± 10⁶–169.11 ± 10⁹) and showed significant differences among soil environments (Table 1, F = 3.77, P = 0.01). The lowest numbers were found in soils collected from fellfields relative to those collected from moss communities and wetlands. However, the highest numbers of bacteria were found in soils from active penguin colonies regardless of low water content of the ornithogenic soils. Soils from relic penguin colonies had significantly lower numbers of bacteria relative to active colonies, but still very high with values within the range of soils from moss communities and wetlands. The Pearson’s correlations demonstrated positive relationships of bacteria numbers with soil moisture, total C, N and available P (Table 2). This result indicates the importance of soil moisture and organic matter for bacterial abundance.

4. Discussion

4.1. General remarks

We investigated physical, chemical and biological properties of soils in the Edmonson Point area (northern Victoria Land) and their local variability within and among different environments to provide background data for analyses of relationships among soil geochemistry, vegetation, and biotic communities (see Smykla et al., 2010, 2011, 2012; lakovenko et al., in press). Our sampling protocol has been...

62

applied successfully in studies on development and geochemistry of
Antarctic soils (e.g., Lee et al., 2004; Engelen et al., 2008). As in other
Antarctic regions, the soils in the Edmonson Point area were unsorted,
did not have developed soil profiles and, with the exception of the
ornithogenic soils, displayed no visible change in color with respect to
the parent material. Although with some limitations, the collected
data, therefore, may provide important insights on soil development
processes and geochemistry with respect to variation in local environ-
mental conditions.

Our results indicate that the physical, chemical and biological charac-
teristics are highly variable among the many different soil environ-
ments at Edmonson Point, with corresponding significant differences
in the soil characteristics (Table 1). Although highly variable some of
the characteristics showed significant correlations (Table 2) indicat-
ing common drivers for their geochemistry.

In Antarctica the degree of chemical weathering is relatively
small (Campbell and Claridge, 2004; Lee et al., 2004; Navas et al.,
2008) and soil development is largely influenced by physical
weathering related to cryogenic processes resulting from freeze-
thaw cycles. Disintegrating bedrock supply material for soil develop-
ment (Schaef er et al., 2008), and thus soil characteristics are deter-
mined primarily by parent materials (Campbell and Claridge, 1987;
Cannone et al., 2008; Navas et al., 2008; Simas et al., 2008). The
parent materials in the Edmonson Point area are relatively homogenous
and consist mostly of weathered and unconsolidated basaltic lavas
and scoria (Baroni and Orombelli, 1994; Harris and Grant, 2003).
Thus, all the sites investigated during the present study were compara-
tile in terms of parent materials. Therefore, high variation in phys-
ical and chemical properties among particular soil environments of
the Edmonson Point area cannot be related to differences in compos-
tion of their parent materials, and must be driven by other environ-
mental and/or biotic factors.

Our results also demonstrate that the most significant differences
encountered in soil characteristics among local environments are rel-
ted to past and present activity of penguins. This finding is consistent
with previous investigations on the formation of ornithogenic soils
caused by enrichment of the ground from penguin guano, resulting in
a soil that is distinctly different from the mineral, generally nutrient
poor Antarctic soils (Ugolini, 1972; Speir and Cowling, 1984; Tatur
and Myrcha, 1984; Heine and Speir, 1989; Tatur, 1989, 2002; Myrcha
and Tatur, 1991; Emслиe et al., 2014).

4.2. Ornithogenic soils

Characteristics of the investigated ornithogenic soils were in
close agreement with other studies in Antarctica (i.e., Campbell and
Claridge, 1966; Ugolini, 1972; Speir and Cowling, 1984; Heine and
Speir, 1989; Hofstee et al., 2006). These soils are generally rich in car-
bon (C), nitrogen (N), phosphorus (P) and other bio-elements
(i.e., Ca, K, Mg, Na), with low C/N, high electrical conductivity (EC)
and large variation in pH values. Their contents of inorganic micro-
and macro-elements are also strongly different, with considerably
higher values of several so-called penguin bio-elements (see Liu
et al., 2013). Biological properties (i.e., chlorophyll content and bac-
teria numbers) of ornithogenic soils were also markedly different
(Table 1) and showed a high level of interdependence with penguin
bio-elements (Table 2).

Ornithogenic soils develop with the continuous addition of fresh
guano to the surface that in turn alters soil processes leading to remod-
eling of the soil profile and profound changes in soil properties. In
Antarctica, ornithogenic soils have a distinct morphology and are read-
ily distinguished by their discrete coloration, presence of nesting pebb-
les (rounded or subangular gavels and stones mainly 10–40 mm in
 diameter) and penguin remains (bones, feathers, egg shells and even
complete or partial mummies) throughout the profile (Campbell and
Claridge, 1966; Ugolini, 1972; Speir and Cowling, 1984; Heine and
Speir, 1989; Tatur and Myrcha, 1984; Tatur, 1989, 2002; Sun et al., 2013; Emslie et al., 2014).

At active penguin colonies at Edmonson Point the ground was covered with a compacted, dried layer of light brown guano and pebbles forming visible nests (Fig. 2e). The underlying guano layers were dark brown with a very sticky and greasy consistency and had a characteristic strong ammonia odor. Soils at relict penguin colonies differed markedly from those at active colonies. The ground was completely covered with lag pavement of loose nesting pebbles without any visible signs of abandoned nests. These areas also lacked the original guano crust, which has eroded and/or washed away over many years after penguins deserted the colony. The buried guano layers (Fig. 2f) were reddish- to yellowish-brown in color, very dry and dusty throughout the profile and had no ammonia smell. Such characteristics are consistent with the sequence of changes related to the age of ornithogenic soils and their biochemical and biological activity reported from Inexpressible Island (Campbell and Claridge, 1966) and Cape Royds (Heine and Speir, 1989).

Although ornithogenic soils are often over 50 cm deep and sometimes may even accumulate to depths of several meters (Campbell and Claridge, 1966; Tatur, 1989; Speir and Cowling, 1984; Emslie and Woehler, 2005), the ornithogenic soils at Edmonson Point investigated here were only ~20 cm deep (Emslie et al., 2007). The ornithogenic layers did not show any obvious signs of cryoturbation either within the guano horizons or between the guano and underlying mineral horizons. As suggested by Heine and Speir (1989), lack of cryoturbation in ornithogenic soils could result from lowering of freezing point by their high salt content and heat absorption capacity. Adélie penguins usually establish their colonies on exposed ridge crests and mounds, which because of their higher position in the landscape become snow-free and dry, and thus available for nesting early in the summer season. Thus, aridity of penguin nesting sites may also contribute to lack of cryoturbation in ornithogenic soils. However, the lack of cryoturbation is a specific feature of the ornithogenic soils only in dry conditions of the continental Antarctic. Under the humid climate of the maritime Antarctic, intense cryoturbation and water percolation incorporates penguin guano deep into the soil profile leading to essential remodeling of underlining mineral horizons (Tatur, 1989, 2002; Myrcha and Tatur, 1991; Tatur et al., 1997; Michel et al., 2006).

In the maritime Antarctic high water availability and relatively high temperatures also favor rapid decomposition of fresh penguin guano. Due to microbiological mineralization, over 30% of C and 50% of N in the guano can volatilize to the atmosphere within the first month of deposition (Zdanowski et al., 2005). Gradual decomposition of organic matter continues with time resulting in pronounced alternation of physical and chemical properties of ornithogenic soils (Tatur, 1989, 2002; Myrcha and Tatur, 1991; Tatur et al., 1997). After penguins desert their colony, the surface guano is strongly reduced by wind weathering and/or snowmelt and precipitation that dissolves and washes away the uppermost layers of the guano, exposing lag pavement of loose nesting pebbles. Chemical changes in ornithogenic soils are initially reflected by the lowering in EC, N and C values, the increase in pH and P levels and consequently by reduction of the C/P and N/P ratios (Tatur, 1989, 2002; Myrcha and Tatur, 1991; Tatur et al., 1997; Zdanowski et al., 2005; Michel et al., 2006; Simas et al., 2008). However, the exposed pebbles are quickly colonized and overgrown by vegetation leading to deposition of organic matter and formation of a black humus layer that contains high C/N and C/P ratios and low pH typical of humified plant material (Tatur et al., 1997; Michel et al., 2006).

In the ornithogenic soils at Edmonson Point, contents of N and C also declined with time. But C/N ratios did not differ between soils from occupied and relict colonies demonstrating that during decomposition processes both N and C are lost at comparable rates. During that process ornithogenic P is not as readily lost as N and C, resulting in high reduction of N/P and C/P ratios. The lack of changes in C/N and pH values also reflects the lack of enrichment with vegetation-derived C. Relict penguin colonies at Edmonson Point were occupied by penguins from approximately 1630 to 1220 years before present (B.P.; Emslie et al., 2007). Still, only single small thalli of nitrophilous lichens and alga Prasiola crispa were found growing at these colonies. Such scant vegetation may be due to local environmental constraints and/or too little time for vegetation development since these colonies were abandoned by penguins. Observations at nearby relict penguin colonies at the Northern Foothills (Smykla et al., 2011), where there is a much older occupation history dated at 7060–2960 years B.P. (Emslie et al., 2007), indicate that diverse assemblages of nitrophilous lichens may gradually overgrow the nesting pebbles. In addition, cushions of mosses can also develop among the pebbles. Although vegetation at relict penguin colonies at the Northern Foothills was more diverse (Smykla et al., 2011) it was still scarce and the pavement of nesting pebbles was clearly visible. It seems, therefore, that in Victoria Land even several thousand years after penguins abandon their colonies the contribution of vegetation to geochemistry and development of the relict soils is negligible.

While vegetation within relict penguin colonies in Victoria Land is at best very scant, high levels of chlorophyll and bacteria exist in the ornithogenic soils (Table 1) and indicate the presence of rich and biologically functioning assemblages of soil microflora. Surprisingly, although these soils had very low water content, the amount of total chlorophyll both in soils from active and relict colonies was marginally higher than in wetland soils (Table 1). This result suggests potentially high primary productivity of the ornithogenic soil microflora. However, the lack of changes in C/N and pH values indicates that the relative contribution of this rich microflora to the organic matter composition is very low.

On the other hand bacteria numbers and changes in chemical properties of ornithogenic soils indicate high importance of soil microflora in decomposition and nutrient mineralization processes. In soils from active colonies bacteria numbers were very high, but in soils from relict colonies they were considerably lower and comparable to values from moss communities and wetlands (Table 1). Very high bacteria numbers found in soils from active colonies, together with depletion over time of C and N soil contents, demonstrate that decomposition and mineralization processes of the organic matter in these soils are relatively active, but with time they decrease considerably to levels comparable to other soil environments. This result is consistent with other studies which reported very high bacteria abundance and activity in soils with fresh guano input (Orchard and Corderoy, 1983; Ramsay, 1983; Ramsay and Stannard, 1986; Roser et al., 1993; Tscherko et al., 2003; Zdanowski et al., 2005; Aislabie et al., 2009), whereas after cessation of guano inputs there was a significant decrease in soil bacteria abundance and activity rate (Orchard and Corderoy, 1983; Ramsay, 1983; Roser et al., 1993; Aislabie et al., 2009), often to levels found in other soil environments.

4.3. Mineral soils

Because soils in the Edmonson Point area have permafrost in the upper 100 cm (Bargagli et al., 1999; Harris and Grant, 2003; Cannone et al., 2008; Cannone and Guglielmin, 2009) and the upper portion of their profile freezes and thaws periodically, they can be classified as Cryosols by World Reference Base for Soil Resources (Kimble, 2004) or Gelisols as defined by USDA Soil Taxonomy (Beyer et al., 1999). While the classic soil-forming factors of climate and topography, vegetation, soil biota, and time each play a role in the development of permafrost-affected soils, they are defined entirely by their thermal conditions and water is considered one of the most significant factors influencing processes in their pedogenesis and evolution (Campbell and Claridge, 1987; Kimble, 2004; Bockheim, 2008). The availability of moisture also has been recognized as the primary driver for biological processes in Antarctic soils (Kennedy, 1993; Ellis-Evans, 1997; Wynn-Williams et al., 1997; Barrett et al., 2006a, 2006b). It is not surprising, then, that numerous characteristics of the investigated soils showed significant correlations with the soil water content (Table 2). Thus, in the absence
of significant differences in the soil parent materials, variation in characteristics and development of mineral soils in the Edmonson Point area are driven primarily by hydrology and associated biological processes. The water contents of the mineral soils we investigated ranged from 3.1 to 210.7% of soil dry weight with very high differences in moisture among particular soil environments (Table 1). Previous investigations conducted in the Edmonson Point area also reported high variability in the soil water contents (Wynn-Williams et al., 1997; Bargagli et al., 1998, 1999; Lewis Smith, 1999; Cannone et al., 2008; Cannone and Guglielmin, 2009; Malandrino et al., 2009), with the highest values exceeding 450% in soils under cyanobacterial mats (Lewis Smith, 1999). These are very high values when compared to data reported in majority of other studies. For example, in coastal ecosystems of McMurdo Sound soils on average contain only about 5% of moisture. Soils of inland regions at higher altitudes have even lower moisture contents and dramatically more xeric conditions occur in soils of the neighboring McMurdo Dry Valleys, where moisture values are usually lower than 1% (Campbell et al., 1997; Campbell and Claridge, 2004; Aislabie et al., 2009). The Dry Valleys are characterized by katabatic winds blowing seaward from the plateau so that most of the snow that falls on the ground is removed by this wind or sublimates, ensuring cold and very dry climatic conditions. Consequently melt-water is rare and soil moisture levels are very low (Campbell et al., 1997; Barrett et al., 2006a; Malandrino et al., 2009).

Malandrino et al. (2009), reported very low moisture values (i.e., 0.25–1%) in soils of Edmonson Point area also indicating very arid climatic and environmental conditions. However, contrary to his hypothesis, results presented here and in other studies (Wynn-Williams et al., 1997; Bargagli et al., 1998, 1999; Lewis Smith, 1999; Harris and Grant, 2003; Cannone et al., 2008; Cannone and Guglielmin, 2009) demonstrate the occurrence of exceptionally high water abundance in soils of this area. As indicated by Campbell and Claridge (1987) in coastal ice-free areas of northern Victoria Land (i.e., Cape Hallett, Edmonson Point), due to warmer climate and protection from the katabatic winds, snow tends to melt rather than sublimate. Moreover, easterly winds and oceanic air masses with accompanying low clouds and maritime aerosol also bring additional moisture. Therefore, in soils of coastal regions of northern Victoria Land in comparison with inland ice-free areas and sites in southern Victoria Land, in general significantly greater quantities of water are available (Campbell and Claridge, 1982, 1987; Barrett et al., 2006a; Bockheim, 2008).

There is, however, very high temporal variability in soil water content throughout the season (Wynn-Williams et al., 1997; Lewis Smith, 1999) which might explain exceptionally low values of soil moisture recorded by Malandrino et al. (2009). The dark ground encourages rapid snowmelt in spring providing high abundance of water. After snowmelt ephemeral melt-water streams and ponds are common, and soils become saturated with groundwater. However, with the onset of summer most of the snow melts and disappears (Harris and Grant, 2003). Moreover, as the soil coarse structure and high stone content provide only low water holding capacity (Campbell and Claridge, 1982, 1987) water from the snowmelt quickly drains and/or evaporates. This mechanism can probably explain the negative correlation of soil water content with the amount of gravel (Table 2). As a consequence with the onset of summer season barren coarse-grained soils desiccate to their typical low water content (Wynn-Williams et al., 1997; Lewis Smith, 1999), with moisture values dropping only to ~1% of their springtime maxima (see Table 1 in Wynn-Williams et al., 1997). At this time, most of the Edmonson Point area becomes dry (Harris and Grant, 2003), but depressions underlying permafrost act as a barrier for water movement, creating restricted drainage with wet morphology such as seepages, ponds and lakes (Campbell et al., 1997; Moodhead et al., 2003). The moisture characteristics of the soil at any particular site are, therefore, governed by specific site features, such as topography and proximity to water source. Sampling may, however, often provide no more than a snap-shot of temporal variability in local hydrological processes. Despite this variability, the strong correlations between soil water content and numerous soil characteristics (Table 2) indicate that our data may be considered representative of the local variability, covering a wide range of hydrological gradients that provide insight on the assessment of local biogeochemical processes.

Although the soil profile structure was not analyzed, our data provide also insight on the soil developmental processes. Soils at fellfields appear to be the most immature, as indicated by the presence of more coarse-grained material. Other criteria that support this conclusion include a pH near neutral, very low EC, and only trace amounts of C and N with a relatively low C/N value (Table 1). These characteristics are similar to other Antarctic soils that are at a very early stage in physical and biological development, such as skeletal soils on very young moraines (Beyer et al., 2000; Tscherko et al., 2003) or inland nunataks (Engelen et al., 2008; Abakumov, 2010). Higher amounts of fine-grained material in moist soils might be related to more effective disintegration of the parent material, due to both enhanced freeze–thaw and chemical weathering processes facilitated by available soil water (Campbell and Claridge, 1982, 1987). However, weathering rates in Antarctic soils are extremely slow (Campbell and Claridge, 1987; Lee et al., 2004). In addition, abundance of soil water has buffering effects and reduces the number of freeze–thaw events (Cannone and Guglielmin, 2009). Therefore it is likely that in the geologically young soils of Edmonson Point the effects of weathering processes are not very pronounced. Sheltered environments, such as moist depressions and small valleys, are obvious sites for the accumulation of windblown materials. Therefore, a greater proportion of finer material found in soils from wetlands and moss communities (Table 1) is an expected result that may be linked with their distinctly higher C and C/N values that result from accumulation of organic matter in concert with very low decomposition rates. The high level of interdependence between pH and C content is also supported by their strong negative correlation (Table 2). The main factors leading to slow decomposition rates in the Antarctic terrestrial ecosystems are unfavorable environmental conditions, such as cold and limited soil moisture (Campbell and Claridge, 1987). The temperature data from Edmonson Point demonstrates that, although average air temperatures during the summer period are below zero, temperatures within the soil profile are primarily above freezing, with average temperatures in wet tundra soils ranging between 2.2 and 3.9 °C and the highest reaching even 18.6 °C (Cannone and Guglielmin, 2009). Not surprisingly the soils we sampled possess abundant microbial flora, which seems to be restricted only by soil water availability. Such high soil temperatures together with high moisture content, rich microbial flora and distinctly lower C/N values compared to southern Victoria Land and inland localities (where soil C/N can reach 87.8, Hopkins et al., 2006) suggest that organic matter decomposition may not be as low as commonly assumed for Antarctic soils. This result is consistent with observations of Cannone et al. (2008) who pointed out that soils with high moisture also have very active decomposition processes. This pattern is probably due to greater abundance and activity of soil microbiota linked to higher summer temperatures and abundance of water. However, further studies are still required to measure the decomposition rates in Victoria Land soils.

Greater N content in soil from moss communities and wetlands (Table 1) may again be linked with higher levels of organic matter and the activity of abundant microflora, which is also supported by their significant correlations (Table 2). In particular, cyanobacteria during the short Antarctic summer are capable of fixing large amounts of atmospheric nitrogen in favorable moisture and temperature conditions, thereby enriching the resultant organic matter with N compounds (Christie, 1987; Bargagli et al., 1999). In Victoria Land the absence of vascular plants and very limited distribution of mosses and lichens render assemblages of these microbiotas as the primary drivers of C and N
cycling, and affects the mineral and biological development of soils. Their importance in soil development is particularly visible in wetlands, where cyanobacteria develop visible mats overgrowing the soil surface (Fig. 2d). Not surprisingly, high chlorophyll content and high chlorophyll a/b ratio (Table 1) also indicate their prevalence in the topsoil. Due to abundant cyanobacteria, wetlands are one of the most productive environments in Antarctica and serve as hot-spots of contemporary resources for surrounding polar deserts (Moorehead et al., 2003; Barrett et al., 2006a). Although not so conspicuous, large populations of cyanobacteria are also found growing on moss shoots providing significant amounts of N for moss growth (Christie, 1987). Therefore, as indicated by Bargagli et al. (1999), higher N stocks found in soils from moss communities may be related not only to fixation in soil, but also to leaching from mosses and moss–dwelling cyanobacteria. In feld soil levels of C and N, although very low in absolute terms, are also very likely to be derived in situ from the activity of soil microflora (Engelen et al., 2008). However, these communities are limited by lack of moisture and are very scarce, as indicated by very low bacteria numbers and chlorophyll values (Table 1) and positive correlation of their abundances with soil water content (Table 2). Moreover, they probably remain dormant through most of the year and resume activity only during brief period of snowmelt when the soil briefly becomes saturated with melt-water (Wynn-Williams et al., 1997; Ellis-Evans, 1997; Hopkins et al., 2006; Aislabie et al., 2009). Further evidence of microbial C and N origin in feld soil is that the total C seems to be present only in the organic form as no carbonates were detected in these soils. While C and N contents of the mineral soils seem to be controlled by soil biology, accumulation and geochemical cycling of other elements are known to be driven by a suite of physical factors, such as parent material, degree of mineral weathering, and external inputs (Campbell and Claridge, 1987; Barrett et al., 2006a). As indicated above, Edmonson Point soils all have a common parent material and are geologically young. Therefore, external inputs, rather the parent material or differences in weathering rates, seems to be the primary mechanism accounting for differences in elemental composition among the investigated soil environments.

Here, we found that soils from feld and moss environments are very similar in elemental composition (Table 1). In general, concentrations of the majority of bio-elements (i.e., Ca, K, Na, Mg) from these environments had the lowest values among all the investigated soils, with concentrations corresponding to typical background values for Antarctic soils developed on similar bedrock (e.g., Cannone et al., 2008; Bargagli et al., 1999; Malandrino et al., 2009; Liu et al., 2013). According to Bargagli et al. (1999) moss beds can significantly modify the chemistry of the soil, not only by fixing C and providing an environment for N fixing cyanobacteria, but also through altering migration of ions in the soils. Absorbing water from the soil mosses enhance the upward migration of salt solutions and accumulate major and trace elements, decreasing their concentrations in the underlying soil. However, our study did not show any effects of mosses on soil elemental composition (Table 1). Bargagli et al. (1999) analyzed the top layer of soil up to 5 cm deep and found that alternation of soil elemental composition by mosses is restricted to the uppermost layer of the topsoil. Thus, lack of evidence of such processes here may be due to differences in the depth of the soil sample collection.

Alternatively, wetland soils showed elevated concentrations of the investigated bio-elements (Table 1). As indicated above, wet depressions accumulate windblown fine grained materials. Moreover, due to their restricted drainage wet depressions also collect snowmelt and melted groundwater with dissolved elements from the surrounding areas. As a consequence they accumulate high concentrations of numerous major and trace elements and have very different soil characteristics from these of surrounding areas (Campbell and Claridge, 1982).

Although some amounts of the elements may originate from substratum weathered within the catchment area, proximity to marine resources and aerial deposition are often indicated as important sources of external inputs (Bargagli et al., 1999; Barrett et al., 2006a; Malandrino et al., 2009). According to Bargagli et al. (1999) major ions in snow, melt-water and groundwater extracts in the Edmonson Point area are indeed predominantly of marine origin. Due to proximity to the sea, these inputs may occur directly through the marine aerosols during summer storms and/or through snow blown off the sea ice. On the other hand ornithogenic soils are also known as an important source of marine-derived elements for terrestrial environments (Myrcha and Tatur, 1991; Tatur et al., 1997; Tatur, 2002; Zdanowski et al., 2005; Liu et al., 2013). Strong winds can transport and widely redistribute small particles of eroded guano over the entire surrounding area. Moreover, the topographical features of the penguin colonies enable downward migration of snowmelt loaded with guano solutions to surrounding soils. Finally, percolating through the soil, snowmelt and groundwater may transport and deposit dissolved elements into undrained wetland soils and lacustrine environments. Thus, the elemental composition in the investigated wetland soils seems to be strongly altered by deposition of the elements transported not only from their drainage area, but also by biogeochemical processes in the whole surrounding area. These soil environments, therefore, provide a source of valuable records that may facilitate understanding of geochemical and environmental processes in the Antarctic terrestrial ecosystems.

Acknowledgments

The first author would like to thank the Directors of the Department of the Antarctic Biology Polish Academy of Sciences, Stanislaw Rakusa-Suszczewski, Andrzej Tatur and Katarzyna Chwedorzewska, for their cooperation and support provided on behalf of the Polish Antarctic Program. Thanks are due to Eva Kašťovská, Ondrej Komárek, Justyna Morawska-Fliszonka, Hana Šantrůčková and Szymon Wójcik for the laboratory support and/or assistance. We would also like to express our special thanks to Larry Coats for comradeship and assistance during the field survey, and to the personnel of the U.S. Antarctic Program at McMurdo Station and the Italian National Program for Antarctic Research (PNRA) at Mario Zucchelli Station at Terra Nova Bay for logistical aid. This work was completed within the project of the senior author funded by the Polish Ministry of Science and Higher Education within the program Supporting International Mobility of Scientists and within grant nos. 2P04F00127, NN304069033, NN305376438 and NN304014939. This work was also partly supported under the agreement on scientific cooperation between the Polish Academy of Sciences and the Academy of Sciences of the Czech Republic within the project “Soil biodiversity of the Antarctic terrestrial ecosystems”. The field survey was made possible with funding to S. Emslie from the National Science Foundation (ANT 0739575) and through logistical support supplied by Raytheon Polar Services.

References


