# Biological soil crusts in continental Antarctica: Garwood Valley, southern Victoria Land, and Diamond Hill, Darwin Mountains region

CLAUDIA COLESIE<sup>1</sup>, MAXIME GOMMEAUX<sup>2</sup>, T.G. ALLAN GREEN<sup>3,4</sup> and BURKHARD BÜDEL<sup>1</sup>

<sup>1</sup>Plant Ecology and Systematics, University of Kaiserslautern, PO Box 3049, 67653 Kaiserslautern, Germany <sup>2</sup>GEGENAA, EA 3795, Université de Reims Champagne-Ardenne, 2 Esplanade Roland Garros, 51100 Reims, France <sup>3</sup>Departamento de Biologia Vegetal II, Universidad Complutense, 28040 Madrid, Spain <sup>4</sup>Department of Biological Sciences, University of Waikato, Private Bag 3105, 3240 Hamilton, New Zealand claudia.colesie@biologie.uni-kl.de

**Abstract:** Biological soil crusts are associations of lichens, mosses, algae, cyanobacteria, microfungi and bacteria in different proportions forming a thin veneer within the top centimetres of soil surfaces. They occur in all biomes, but particularly in arid and semi-arid regions, even in the most extreme climates. They carry out crucial ecosystem functions, such as soil stabilization, influencing water and nutrient cycles, and contribute to the formation of microniches for heterotrophic life. In continental Antarctica especially, these roles are essential because no higher plants provide such ecosystem services. We provide a detailed description of biological soil crusts from Garwood Valley, McMurdo Dry Valleys region (78°S) and Diamond Hill (80°S) in the Darwin Mountains region. The coverage was low at 3.3% and 0.8% of the soil surface. At Garwood Valley the crusts were composed of green algal lichens, cyanobacteria, several species of green algae and the moss *Hennediella heimii* (Hedw.) R.H. Zander. Diamond Hill crusts appear to be unique in not having any species of cyanobacteria. Major parts are embedded in the soil, and their thickness correlates with higher chlorophyll contents, higher soil organic carbon and nitrogen, which are fundamental components of this species poor cold desert zone.

Received 17 October 2012, accepted 30 March 2013, first published online 23 May 2013

Key words: ecosystem functioning, lichens, McMurdo Dry Valleys, mosses, soil organic carbon contents, soil stabilization

## Introduction

Biological soil crusts (BSC) are intimate associations between soil particles, cyanobacteria, algae, microfungi, lichens and bryophytes and are found worldwide in arid and semi-arid regions, or where higher vegetation is sparse or absent (Belnap et al. 2001). In such regions the magnitude of environmental impacts is affected by these surface communities (Pointing & Belnap 2012). In particular, BSC can improve the stability of soils, for example by increasing the resistance to soil erosion by wind as the BSC develop. Biological soil crusts also increase soil fertility and influence hydrological cycles (Belnap & Lange 2001). By fixing atmospheric carbon during photosynthesis the photoautotrophic components of the BSC can underpin the trophic hierarchy by leaching some fixed carbon into the soils (Dudley & Lechowicz 1987) and by themselves being a food resource for heterotrophs. Mosses in particular are known to contribute considerably to the total carbon pools in high arctic desert soils (Arndal et al. 2009). In addition, some BSC components can also fix atmospheric nitrogen, with bryophyte-cyanobacterial associations playing an important intermediate role in this process in polar environments (Stewart *et al.* 2011). In these environments the quantity of nitrogen fixed is known to be adequate to support the nitrogen needs of mosses and vascular plants (Dickson 2000), and to supply biological soil crust communities (Breen & Levesque 2008). For continental Antarctic environments hypolithic communities are especially important contributors to the fixed nitrogen budget in the soils (Cowan *et al.* 2011).

Ice-free areas in Victoria Land, Antarctica, especially the McMurdo Dry Valleys with an area of 6861 km<sup>2</sup>, represent over 15% of the ice-free land on the Antarctic continent (Antarctic Specially Managed Area (ASMA) No. 2). These ice-free areas are cold deserts with low precipitation, high sublimation rates, nutrient poor soils and few species. Due to these harsh environmental conditions, no vascular plants or vertebrates inhabit the Dry Valleys and soils in this region were widely presumed to be almost sterile (Horowitz *et al.* 1972). More recent investigations using molecular microbiological methods have dramatically improved our knowledge and it is now well established that microbial communities are present in almost all soils (Cary *et al.* 2010). In this extreme ecosystem, temperature, moisture and organic matter availability are low while

Fig. 1. Map of the western Ross Sea coastline (right side of figure) showing the locations of the two research sites, McMurdo Dry Valleys and Diamond Hill, with an inset (top right) showing the Ross Sea location in Antarctica. Detailed maps of the two research areas are in insets on the left side of the figure. In the latter two insets the red dot marks the research sites, brown areas are ice-free land and the blue lines the coastline. Maps downloaded from the SCAR Antarctic Digital Database (November 2012).

salinity is often high. As a result, the biomass and diversity of photoautotrophic organisms is generally low (Barrett *et al.* 2006). Glacier runoff, meltwater lakes and other areas with a relatively consistent water flow in summer are exceptions and can have a visible surface cover of mosses, lichens, algae and cyanobacteria (Green & Broady 2001). The biota in the McMurdo Dry Valleys have been recently reviewed (Barrett *et al.* 2006, Cary *et al.* 2010).

The concept of BSC as a photoautotrophic community has been rarely applied in Antarctica (Green & Broady 2001) despite the probability that it might be a highly suitable environment for this life form. Until now studies on terrestrial vegetation in ice-free Antarctic areas have mainly concentrated on taxonomic problems culminating in floras for the bryophytes (Ochyra *et al.* 2008) and lichens (Øvstedal & Smith 2001). Studies on community form have been rarer and have been based on life form and structure (Longton 1973, Schwarz *et al.* 1992, Seppelt *et al.* 2010).

Here we study the composition, the structure and the distribution of BSC in two ice-free areas on the central Ross Sea coastline. The first is on the floor of Garwood Valley in the Dry Valleys of southern Victoria Land. The second is at Diamond Hill in the Darwin Mountains region, which is at least as extreme, possibly more so, than the Dry Valleys. Terrestrial biology has been poorly studied in

this area. We describe the abundance, the coverage, the composition, the influence on substrate stabilization, the formation of microhabitats for heterotrophic species, and the structure of BSC found in the two areas in order to gain a better appreciation of the role of BSC in these extremely depauperate soils.

#### Material and methods

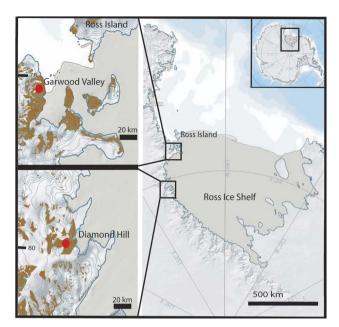
#### Field sites

Diamond Hill (79°50'30.2"S, 159°21'04.2"E), Brown Hills, Darwin Mountains region was visited in January 2009 (Fig. 1). The immediate vicinity of the Diamond Hill site is dominated by outcrops of granites, granodiorites and high-grade metamorphic rocks, dated as Cambrian and Ordovician (Carosi et al. 2007). Further inland the Beacon Sandstones (Devonian-Triassic) are intruded by sills and dikes of tholeiitic dolerite of Lower Jurassic age, which are related to the Ferrar Large Igneous Province (Elliot & Fleming 2004). Cosmogenic exposure ages of exposed surfaces in the vicinity range from 1000 to 1 million years, and the Diamond Hill site is estimated to have a surface age of about 400 000 years (Storey et al. 2010). Mean soil moisture content is  $3.04 \pm 2.37\%$  (g g<sup>-1</sup>) (Magalhães *et al.* 2012). A recent study on biotic diversity showed a trend of very low lichen and algae species diversity and total absence of any bryophyte (Magalhães et al. 2012).

Garwood Valley (78°01'23."S, 163°53'24.2"E), McMurdo Dry Valleys, southern Victoria Land was visited in December 2009 and January 2010 (Fig. 1). The Garwood Valley site is dominated by outcrops of granites and gneisses, together with amphibolites, marble and dolomites. The valley floor is covered with glacial drift of several ages ranging from 22 000 to 35 000 years. Soil moisture content in the valley floor is 26.83  $\pm$  8.49% (gg<sup>-1</sup>) (recalculated from Gregorich *et al.* (2006), assuming 1 m<sup>3</sup> granite gravel = 1.8 t). For a detailed description of the sampling site see Elberling *et al.* (2006). Vegetation in this maritime-associated valley is relatively rich with up to 15 lichen species (Pérez-Ortega *et al.* 2012) and mosses like *Hennediella heimii* (Hedw.) R.H. Zander or *Bryum argenteum* Hedw.

#### Sampling and coverage analysis

The visit to Diamond Hill lasted only three instead of the initially-planned fourteen days because of severe weather conditions. As a result, only a rapid assessment with sampling was possible. Every BSC detected was sampled (n = 15) during a 16 km walk over a homogenous area on the north slope of Diamond Hill at a mean altitude of around 400 m. The sampled area was dominated by granodioritic orthogneisses as rock cliffs, and large and small boulders. Although the previously designed random sampling procedure was not possible, the sampling carried



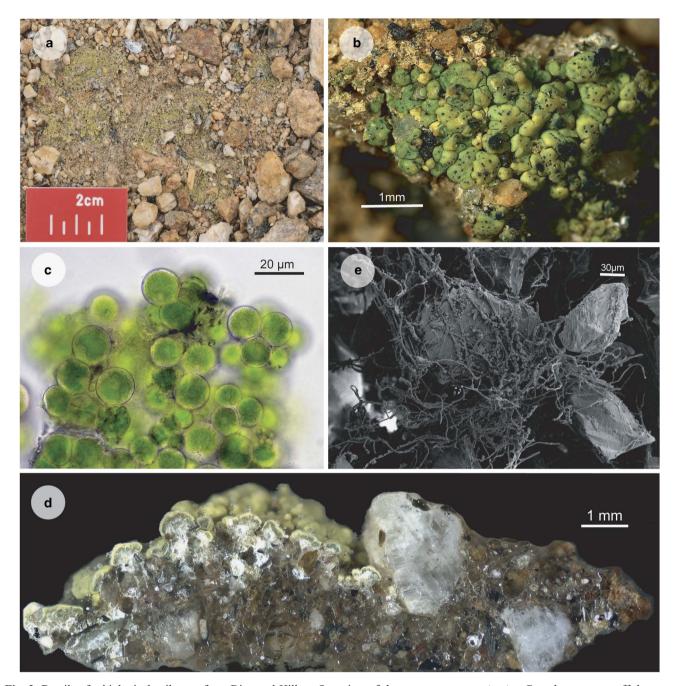


Fig. 2. Details of a biological soil crust from Diamond Hill. a. Overview of the crust appearance *in situ*. Gravel was swept off the crust to make it visible as a greenish tinge to the soil surface. b. The lichen *Acarospora gwynnii* (16x). This green algal lichen dominates the biological soil crusts at Diamond Hill. c. Isolated green algae (*Trebouxia aggregata* (Archibald) Gärtner).
b. and c. were obtained using light microscopy (40x). d. Embedded cross-section of a polished block of the whole biological soil crust. *Acarospora gwynnii* sitting on the top of the substrate and white medulla and rhizines penetrating into the soil. e. LT-SEM shot of *Acarospora gwynnii* rhizines with adhering single soil particles inside the crust. Scale bars are included in each picture.

out can be considered random as distance and direction of the walk was undirected. Biological soil crusts coverage was estimated by surveying a 600 m radius circle for BSC in detail, and estimating coverage visually. This coverage value cannot be statistically supported, but represents an approximate estimation. In Garwood Valley the BSC coverage was checked across the whole area of the valley floor using a random generator, adapted from a "blind man's bluff"-based sampling approach as follows: a sampling grid  $(25 \times 25 \text{ cm})$  was thrown with random distance, direction and angle from last sampling point and checked for BSC occurrence using the point intercept method (Fig. 2a); this allows you to extrapolate the data to encompass the complete area. Every detected BSC was sampled (n = 30).

## Sampling procedure

The structures of representative samples of the BSC were investigated using several different light microscopy techniques (Axioskop and Stemi 200-C, Carl Zeiss, Jena, Germany). The vertical structure of the BSC within the soil was determined using samples prepared as follows: crust samples ranging from 0.5-3 cm in size were placed in Teflon moulds and soaked with Geofix two-component epoxy resin (Société d'Equipement Scientifique et Industriel Lyonnais (ESCIL), Chassieu, France). After hardening, the sample was cut using a diamond saw and the cut side polished twice. Selected samples were kept with only one polished side and observed using reflectedlight optical microscopy and scanning electron microscopy (SEM). Other samples were cut and polished to a thickness of c. 30 µm. These samples were viewed using transmittedlight optical microscopy and SEM. For each BSC, the thickness above and below the soil surface was measured using the AxioVision software (Carl Zeiss, Jena, Germany). Mean values for three Garwood samples (seven measurements for each sample) and mean values for three Diamond Hill samples (five measurements for each sample) were calculated. Using this data the above/below ground ratio (A/B<sub>ratio</sub>, mm/mm) of the BSC was then computed. All values were compared using Student's t-test.

In addition, low temperature scanning electron microscopy (Supra 55VP, Carl Zeiss, Oberkochen, Germany) was used to study fully hydrated BSC. The samples were frozen in liquid nitrogen slush (K1250X Cryogenic Preparation System, Quorum Technologies, Ashford, UK) and mounted on special brass trays for microscopy at -150°C.

Chlorophyll contents were determined by extracting the samples twice with dimethyl-sulfoxide (DMSO) at 60°C for 90 minutes and measuring the absorption at standard wavelengths (n = 3 for the Diamond Hill samples, n = 6 for the Garwood Valley samples).

Soil organic carbon (SOC) content and nitrogen content of the samples were measured after drying the samples (n = 3 for each valley) at 105°C for one hour. Previous microscopic analysis had shown that the thickness of the samples was sufficient to include all photoautotrophic components. Once dry, each sample was homogenized with an agate mortar and analysed for CHN with a Vario Micro Cube (Elementar Analysensysteme GmbH, Hanau, Germany). After the analysis, each sample was heated (120°C) in 10% HCl until fumes were emitted and then reanalysed for CHN. The difference in carbon content was regarded as the organic carbon content. The results were subjected to Student's *t*-test.

The moss species were determined by Rod Seppelt (Tasmanian Herbarium, Hobart, Australia) and names are according to Ochyra *et al.* (2008). Lichen species were determined using the identification guide of lichens in Øvstedal & Smith (2001). Cyanobacteria and algae were identified by direct light microscopy of soil samples and appropriate determination keys (e.g. Ettl & Gärtner 1995, Komárek & Anagnostidis 1999, 2005).

The substrate of the BSC was analysed by microscopic investigation of thin sections and polished blocks prepared as described above. Transmitted-light observations were performed both with a single polarizer and with crossed polarizers. SEM (Hitachi TM1000, equipped with energydispersive X-ray spectroscopy (Oxford Instruments)) investigations were performed on the polished blocks and thin sections with no further treatment.

## Results

## Field sites, organisms and characteristics

Biological soil crusts were found at both sites, Diamond Hill and Garwood Valley. Biological soil crusts in Diamond Hill are dominated by the lichen species *Acarospora gwynnii* C.W. Dodge & E.D. Rudolph (Fig. 2a & b) and green algae of the genera *Diplosphaera*, *Heterococcus*, and *Trebouxia* sp. (Fig. 2c). No other photoautotrophic organisms (neither mosses nor cyanobacteria) are involved in the formation of

**Table I.** Comparison of morphological and physical characteristics of biological soil crusts from Diamond Hill region and Garwood Valley. Shown are mean  $\pm$  SD and significance values from *t*-tests. BSC = Biological soil crusts.

BSC appearance and characteristics			Significance of difference between Diamond Hill and Garwood Valley soil		
Parameter	Diamond Hill	Garwood Valley	t	df	Р
Coverage (%)	0.80	3.31			
Above ground layer (mm)	$3.74 \pm 1.29$	$4.52\pm1.83$	1.2	32	0.23
Soil penetration depth (mm)	$7.76 \pm 2.18$	$23.35 \pm 5.83$	12.21	32	0.0001
Above ground/below ground ratio	$0.50\pm0.18$	$0.17\pm0.11$	-6.52	32	0.0001
Organic carbon content (mg org. Cg <sup>-1</sup> soil)	$0.46\pm0.25$	$1.84\pm0.47$	-4.407	4	0.011
Organic carbon content (g m <sup>-2</sup> )	73.68 ± 15.98	99.31 ± 23.00	-1.58	4	0.18
Total N (mg N g <sup>-1</sup> soil)	$0.10\pm0.01$	$0.14\pm0.08$	1.48	4	0.21
Total N (gm <sup>-2</sup> )	$12.6\pm0.09$	$7.69\pm4.59$	-0.71	4	0.51
Chlorophyll content (mg Chl $a + b$ m <sup>-2</sup> )	$27.79\pm5.34$	$36.0\pm14.33$	1.401	9	0.194



**Fig. 3.** Details of a biological soil crust from Garwood Valley. **a.** Typical *Nostoc commune*-dominated mat occurring in the meltwater streams in Garwood Valley. At the front the sample grid (5 x 5 m, ropes) and small sample grid (25 x 25 cm, metal grid) for coverage determination. **b.** Overview of the crust appearance *in situ*. The BSC is dominated by mosses with the lichens (*Caloplaca citrina*, centre and *Lecanora expectans*, right upper corner) growing on the top of them. **c.** Lateral view on the crusts in a cross-section. Moss stems at the top and moss protonema inside the substrate and the soil. **d.** Overview of *Caloplaca citrina* growing epiphytically on the moss cushions. **e.** Embedded cross-section of a polished block of the whole biological soil crust. Vertical section of lichens growing on the top (arrows) and a massive net of moss and moss protonema throughout the soil. Scale bars are included in each picture.

these crusts. Mean surface area coverage was about 0.8%. One third of the total crust thickness is above and two thirds are below the soil surface giving a A/B<sub>ratio</sub> of  $0.50 \pm 0.18$  (Table I, Fig. 2d). Soil particles adhere to the lichen rhizines building compact aggregations (Fig. 2e). Mean chlorophyll content is  $27.79 \pm 5.34$  mg Chl a + b m<sup>-2</sup>, SOC is  $0.46 \pm 0.25$  mg C g<sup>-1</sup> soil (73.68  $\pm 15.98$  g m<sup>-2</sup>), and total nitrogen content is  $0.10 \pm 0.01$  mg N g<sup>-1</sup> (12.62  $\pm 0.09$  g N m<sup>-2</sup>). The substrate was mainly composed of quartz, calcic and potassic feldspars, pyroxene, amphibole, and biotite.

Biological soil crusts cover an estimated area of 3.31% in the Garwood Valley and are composed of mosses (Hennediella heimii (Hedw.) R.H. Zander), lichens (Caloplaca citrina (Hoffm.) Th. Fr.\*, Lecanora expectans Darb.), green algae (unicellular and immobile) and several species of filamentous and unicellular cyanobacteria. With the exception of BSC along the margins of melt streams, which are dominated by macroscopic mats of the cyanobacterium Nostoc commune Vauch. (Fig. 3a) all soil crusts are dominated by mosses, with lichens only growing on top of the moss cushions (Fig. 3b & c). The two lichen species present are Caloplaca citrina (Fig. 3d), a cosmopolitan species, and Lecanora expectans, an Antarctic endemic. Total BSC thickness is 27.87 mm which is 2.4 times thicker than BSC at Diamond Hill. Penetration into the soil is five times greater than the above ground layer (Table I) giving a A/B<sub>ratio</sub> which is about a third of that at Diamond Hill (Table I). This difference is mainly due to a high amount of moss stems and rhizoids penetrating the soils at Garwood Valley (Fig. 3e). Mean chlorophyll content of these BSC was 33% greater than at Diamond Hill although not significantly different. Soil organic carbon on a dry weight basis was 400% greater than at Diamond Hill (Table I), whereas on an area basis it was only 34% higher. Total nitrogen on a dry weight basis was 40% higher than at Diamond Hill. On an area basis it was about 60% of the Diamond Hill level. Due to a very high variability of the values, none of these results (except the SOC (mg org.  $Cg^{-1}$  soil)) showed statistically significant differences. The substrate at Garwood Valley is mainly composed of quartz, calcite, pyroxene, plagioclase, olivine, amphibole, biotite and calcic plagioclase. Basalt fragments were also observed.

## Discussion

In the present study we have shown that the occurrence of BSC is a general phenomenon in the cold deserts of Victoria Land (Antarctica) with a much wider distribution than previously thought. The few previous studies mainly focused on highly visual biological communities, for example the moss turf cushions at the Canada Glacier flush (Schwarz et al. 1992). The present study extends the known range of BSC further south from the Dry Valleys to the Brown Hills, Darwin Mountains region. The estimated coverage of BSC is not high, being only 3.3% in the Garwood Valley and 0.8% at Diamond Hill. Biological soil crusts in the Garwood Valley have a similar structure to those described from other deserts and are dominated by mosses together with cyanobacteria and algae, any lichens being epiphytic on the moss. Biological soil crusts from Diamond Hill are very different and probably unique. They are dominated by lichens with no mosses and, even more surprisingly, no cyanobacteria. This is in contrast to a recent review, where desert BSC are described as being dominated by cyanobacteria, with their proportion increasing with the harshness of the environment (Pointing & Belnap 2012). Cyanobacteria are also known from some of the harshest environments on earth such as the hyperarid Atacama desert, where they occur hypolithically (Warren-Rhodes et al. 2006). Possible recruitment sources for cyanobacteria are present in the Darwin Mountains area, such as the Lake Wellman area (Webster-Brown et al. 2010, Magalhães et al. 2012), but transfers do not seem to occur. In such high latitude sites terrestrial vegetation becomes confined to microhabitats and biodiversity becomes uncoupled from the macroenvironment and is determined by occasional coincidences of suitable environmental factors (Green et al. 2011). This concept seems to be shown dramatically in this habitat, as the migration of a whole functional group (cyanobacteria) from the recruitment source to the soil crusts is not realized. This may originate either by very narrow suitable life conditions in the microhabitat (open soil without shelter) or by the surrounding climate preventing organisms from migrating.

It is known that cyanobacteria require liquid water in order to become active (Lange et al. 1994) so we suggest that the more extreme aridity and, in particular, the lack of liquid water, is the limiting factor at Diamond Hill, and in the Brown Hills, generally. Bromwich & Guo (2004) modelled precipitation across Antarctica with the Darwin Mountains area (including the Diamond Hill) standing out in their model as having the largest sublimation rates in the Ross Sea region. It is also reported that Diamond Hill has lower atmospheric water vapour pressure (VP) and higher water vapour pressure deficit (VPD) than at Taylor Valley, Dry Valleys, with both sites being at approximately the same altitudes. Soil moisture does not seem to be a suitable water source as soil water contents in Diamond Hill are about one tenth of those in Garwood Valley (Gregorich et al. 2006, Magalhães et al. 2012). The only available source of water for the BSC would be from snowfall and almost all of this occurs at times when the temperatures are well below zero so there is no possibility of liquid water. One possible alternative source of water

<sup>\*</sup> According to Søchting & Castello (2012) in contrast to many reports, the species *Caloplaca citrina* is not to be confirmed for Antarctica. Species assigned to *Caloplaca citrina* from Antarctica refer to either *Caloplaca darbishirei* or *C. soropelta*.

and one that is known to support cyanobacteria in the Dry Valleys, is dew (Büdel *et al.* 2008). However, the dew occurred on endolithic communities embedded in large rocks and the required low temperatures to produce the frost or dew do not appear to occur in soils at Diamond Hill (LGP data, http://www.mcmlter.org/queries/met/ met\_home.jsp, accessed May 2012).

The lack of bryophytes in the BSC from Diamond Hill also support Diamond Hill being a very dry environment. Mosses tend to occur under relatively benign conditions, where liquid water is available (Green & Broady 2001) and are usually considered to be late successional colonizers in BSC (Belnap & Eldridge 2001). By applying the concept of the shoot to root ratio from higher plants to the system of a biological soil crust, Diamond Hill soil crusts are early successional stage crusts as a high allocation to shoot production (above ground layer) is characteristic of vegetation in early successional phases. In contrast, the BSC from Garwood Valley are closer to a climax vegetation phase as they have a high allocation to 'root' (= rhizoids and rhizines) production. Both observations are directly opposite to the reported age of the soils at the research sites (Diamond Hill is around 400 000 years old whilst the floor of the Garwood Valley was under a lake until around 10000 years ago). Two different explanations are available. Either the occurrence of BSC in Diamond Hill is a recent phenomenon generated by small-scale change in climate, or growth conditions in this area are so harsh that development of BSC is nearly impossible. We suggest that the latter explanation is more likely and this would further underline Diamond Hill acting as a migration block along the Ross Sea coastline.

The BSC do appear to provide important ecological inputs in these extreme environments. The organic carbon content of the Garwood Valley BSC investigated in this study is three times the amount previously reported from soils from the same valley,  $0.51-0.62 \text{ mg C g}^{-1}$  (Hopkins et al. 2009). Soil organic carbon of BSC at Diamond Hill is only about 25% of those at Garwood Valley and we assume that inputs would be at least similarly lower because of the much harsher climatic conditions and the strongly restricted activity periods. The difference between the dry weight and area based values for SOC is probably due to a much greater proportion of organic material within the BSC at Garwood Valley. Nevertheless, SOC of the Diamond Hill BSC is still four times higher than in Wright Valley soils without BSC  $(0.11 \pm 0.058 \text{ mg C g}^{-1} \text{ soil})$ , twice that of Victoria Valley soils without BSC  $(0.21 \pm 0.041 \text{ mg C g}^{-1} \text{ soil})$ and four times higher than in Taylor Valley soils without BSC (0.13  $\pm$  0.042 mg C g<sup>-1</sup> soil; Hopkins *et al.* 2009). The occurrence of BSC, therefore, provides an often overlooked carbon source to the soils which is in addition to the legacy carbon (Hopkins et al. 2009).

Organic carbon is not the only ecosystem service that the BSC provide. They can also promote the formation of a soil

ecosystem by providing the initial chlorophyll and nitrogen required. Nitrogen levels are not very different between Garwood Valley and Diamond Hill although the later crust does not contain nitrogen fixing cyanobacteria. We can suggest two possible grounds, not exclusive, for the high nitrogen content in Diamond Hill soils. First, nitrogen could be sourced from endolithic cyanobacteria growing in the surrounding rock boulders. Endolithic coverage is estimated to be 90% of all granite rocks. Second, growth processes may be so slow in the Darwin Mountains BSC that sufficient nitrogen is available from abiotic sources. This non-biological nitrogen uptake was shown to be an important sink in dryland soils (Barrett et al. 2002). Local ponds also have very high nitrate and ammonia concentrations and no nitrogen-fixing cvanobacteria (Webster-Brown et al. 2010), underlining the hypothesis that abiotic nitrogen fixation plays an important role in this environment. If the second suggestion is correct then it is yet another indicator of the extreme conditions in the area. The total nitrogen contents of both BSC investigated in this study is much greater (two to three times) than those reported for the soils without BSC on the floors of other valleys (Table I; Hopkins et al. 2009).

Another ecosystem function that the BSC fulfil is the reallocation of habitats. Biological soil crusts in Garwood Valley contain mosses which are known to form sheltered microhabitats for other organisms like algae, cyanobacteria (Green & Broady 2001), fungi (Fenice *et al.* 1997), tardigrada (Adams *et al.* 2006) and other invertebrates (Schwarz *et al.* 1993). In addition, BSC are well known to play an important role in soil stabilization in other temperate and desert sites and appear to do the same here as the rhizines of the lichens at Diamond Hill, and the moss stems and rhizoids at Garwood Valley, do aggregate the soil particles (Fig. 2f) and will prevent removal by wind. However, the very low coverage for BSC in these extreme sites suggests that the protection effect may not be as strong as in other non-Antarctic BSC sites.

## Summary of BSC in southern Victoria Land

The most eye-catching BSC communities in the Dry Valleys are the bryophyte flushes. They occur at wet sites, particularly glacier melt streams in areas with low water flow, and around meltwater lakes and snow patches (Green & Broady 2001). This BSC type is widespread in the Dry Valley region, for example: Canada Glacier (Schwarz *et al.* 1992), Cape Hallett (Brabyn *et al.* 2006) and Botany Bay (Seppelt *et al.* 2010). Total bryophyte flora in Victoria Land is not rich, being nine species at Botany Bay, three species at Canada Glacier and almost entirely one species at Beaufort Island, out of a total of about 11 species for the entire Ross Sea region (Adams *et al.* 2006).

Beside the mosses, lichens can be major components of BSC. Lichens are not common in the Dry Valleys and

reach a higher species-richness of around 19 species out of a possible nearly 60 species in the Ross Sea region (Cannone & Seppelt 2008), although the exact number is still subject to better collecting and improved taxonomy (Ruprecht et al. 2010). Nearly all are epilithic lichens, but there is a trend in the Dry Valleys and further south for some lichen species to colonize the soil, as found here for Acarospora gwynnii at Diamond Hill. Our study appears to be the first report of lichen-dominated BSC for continental Antarctica, where soil lichens normally grow epiphytically on moss cushions. Only a few species such as Buellia frigida Darb., Buellia grisea C.W. Dodge & G.E. Baker, Buellia pallida C.W. Dodge & G.E. Baker, Carbonea vorticosa (Flörke) Hertel, Rhizoplaca melanophthalma (Ram.) Leuckert & Poelt, Lecidea cancriformis C.W. Dodge & G.E. Baker and Lecidella (Lecidea) siplei (C.W. Dodge & G.E. Baker) May. Inoue, are found growing solitary on soil in protected niches and beneath rocks (Nienow & Friedmann 1993).

The third type of BSC in the Dry Valleys is dominated by cyanobacteria and algae. These crusts (oscillatorialeans like Microcoleus vaginatus (Vauch.) Gom. and chroococcaleans like Gloeocapsa kuetzingiana Naeg.) can be found in more scattered locations like on the lee side of boulders (Green & Broady 2001). Green BSC composed of chlorophytes become prominent where salt and nutrient contents are elevated (Green & Broady 2001). For example, Prasiococcus calcarius (Boye-Pet.) Vischer is known to grow sublithically, associated with bones and mummified seals and birds, and epilithically in summer meltwaters in Victoria Land, the region comprising the Dry Valleys (Broady 1983).

## Conclusions

From this report it becomes obvious that more information is still needed about the presence, distribution, and composition of BSC in ice-free regions of Antarctica in order to understand better their contribution to biodiversity and biocomplexity of Antarctic terrestrial ecosystems. In addition to their role as drivers of biodiversity, BSC may influence soil stabilization of the loose particles of Antarctic soils, and provide new microhabitats for other organisms. In actively fixing carbon dioxide it is likely that they also play a major role in the simply organized food webs by providing an organic carbon supply.

#### Acknowledgements

CC and BB gratefully acknowledge financial support by the Deutsche Forschungsgemeinschaft (DFG SPP 1158, BU 666/11-1+2). This research is part of the New Zealand Terrestrial Antarctic Biocomplexity Survey (NZTABS) and was supported by the New Zealand Foundation for Research Science and Technology (Grant UOWX0710, Understanding, valuing and protecting Antarctica's unique

terrestrial ecosystems: predicting biocomplexity in Dry Valley ecosystems). This paper forms a contribution to the SCAR Programme Evolution and Biodiversity in the Antarctic (EBA) and Antarctica New Zealand's Latitudinal Gradient Project (LGP). Antarctica New Zealand is thanked for providing logistics both for the research in Antarctica and movements to Antarctica and their staff for assisting with removal of equipment. Special thanks to Craig Cary and his team (Biological Sciences, University of Waikato) for the organization and support during the Garwood Valley field trip (K020). We are indebted to Dr Rod Seppelt (Tasmanian Herbarium, Hobart, Australia) for determination of the moss species. Hans Reichenberger is thanked for field and lab assistance. Permits: sampling, entry into protected areas and equipment deployment were approved by the New Zealand authorities. We acknowledge the SCAR Antarctic Digital Database for making the download of the most recent Antarctic maps available online (http://www.add.scar.org/index.jsp). We are grateful to two anonymous reviewers for helpful criticisms on earlier versions of the manuscript.

#### References

- ADAMS, B.J., BARDGETT, R.D., AYRES, E., WALL, D.H., AISLABIE, J., BAMFORTH, S., BARGAGLI, R., CARY, C., CAVACINI, P., CONNELL, L., CONVEY, P., FELL, J.W., FRATI, F., HOGG, I.D., NEWSHAM, K.K., O'DONNELL, A.O., RUSSELL, N., SEPPELT, R.D. & STEVENS, M.I. 2006. Diversity and distribution of Victoria Land biota. *Soil Biology & Biochemistry*, **38**, 3003–3018.
- ARNDAL, M.F., ILLERIS, L., MICHELSEN, A., ALBERT, K., TAMSTORF, M. & HANSEN, B.U. 2009. Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high arctic vegetation types. *Arctic, Antarctic and Alpine Research*, **41**, 164–173.
- BARRETT, J.E., JOHNSON, D.W. & BURKE, I.C. 2002. Abiotic nitrogen uptake in semiarid grassland soils of the U.S. Great Plains. *Soil Science Society* of America Journal, 66, 979–987.
- BARRETT, J.E., VIRGINIA, R.A., HOPKINS, D.W., AISLABIE, J., BARGAGLI, R., BOCKHEIM, J.G., CAMPBELL, I.B., LYONS, W.B., MOORHEAD, D.L., NKEM, J.N., SLETTEN, R.S., STELTZER, H., WALL, D.H. & WALLENSTEIN, M.D. 2006. Terrestrial ecosystem processes of Victoria Land, Antarctica. *Soil Biology* & *Biochemistry*, **38**, 3019–3034.
- BELNAP, J. & ELDRIDGE, D.J. 2001. Disturbance and recovery of biological soil crusts. In BELNAP, J. & LANGE, O.L., eds. Biological soil crusts: structure, function and management (Ecological Studies, 150). Berlin: Springer, 363–385.
- BELNAP, J. & LANGE, O.L. 2001. Structure and functioning of biological soil crusts: a synthesis. In BELNAP, J. & LANGE, O.L., eds. Biological soil crusts: structure, function and management (Ecological Studies, 150). Berlin: Springer, 471–481.
- BELNAP, J., BÜDEL, B. & LANGE, O.L. 2001. Biological soil crusts: characteristics and distribution. *In* BELNAP, J. & LANGE, O.L., *eds. Biological soil crusts: structure, function and management.* (Ecological Studies, 150). Berlin: Springer, 3–31.
- BRABYN, L., BEARD, C., SEPPELT, R.D., RUDOLPH, E.D., TURK, R. & GREEN, T.G.A. 2006. Quantified vegetation change over 42 years at Cape Hallett, East Antarctica. *Antarctic Science*, 18, 561–572.
- BREEN, K. & LEVESQUE, E. 2008. The influence of biological soil crusts on soil characteristics along a high arctic glacier foreland, Nunavut, Canada. Arctic, Antarctic and Alpine Research, 40, 287–297.

- BROADY, P.A. 1983. The Antarctic distribution and ecology of the terrestrial, chlorophytan alga *Prasiococcus calcarius* (Boye Petersen) Vischer. *Polar Biology*, 1, 211–216.
- BROMWICH, D.H. & GUO, Z. 2004. Modelled Antarctic precipitation. Part I: spatial and temporal variability. *Journal of Climate*, **17**, 427–447.
- BÜDEL, B., BENDIX, J., BICKER, F.R. & GREEN, T.G.A. 2008. Dewfall as a water source frequently activates the endolithic cyanobacterial communities in the granites of Taylor Valley, Antarctica. *Journal of Phycology*, 44, 1415–1424.
- CANNONE, N. & SEPPELT, R.D. 2008. A preliminary floristic classification of southern and northern Victoria Land vegetation, continental Antarctica. *Antarctic Science*, 20, 553–562.
- CAROSI, R., GIACOMINI, F., TALARICO, F. & STUMP, E. 2007. Geology of the Byrd Glacier Discontinuity (Ross Orogen): new survey data from the Britannia Range, Antarctica. Related Publications from ANDRILL Affiliates. Paper 19. http://digitalcommons.unl.edu/cgi/ viewcontent.cgi?article=1018&context=andrillaffiliates, 7 pp.
- CARY, C.S., McDONALD, I.R., BARRETT, J.E. & COWAN, D.A. 2010. On the rocks: the microbiology of Antarctic Dry Valley soils. *Nature Reviews*, 8, 129–138.
- COWAN, D.A., SOHM, J.A., MAKHALANYANE, T.P., CAPONE, D.G., GREEN, T.G.A., CRAY, S.C. & TUFFIN, I.M. 2011. Hypolithic communities: important nitrogen sources in Antarctic desert soils. *Environmental Microbiology Reports*, 3, 581–586.
- DICKSON, L.G. 2000. Constraints to nitrogen fixation by cryptogamic crusts in a polar desert ecosystem, Devon Island, N.W.T., Canada. *Arctic, Antarctic and Alpine Research*, **32**, 40–45.
- DUDLEY, S.A. & LECHOWICZ, M.J. 1987. Losses of polyol through leaching in subarctic lichens. *Plant Physiology*, 83, 813–815.
- ELBERLING, B., GREGORICH, E.G., HOPKINS, D.W., SPARROW, A.D., NOVIS, P. & GREENFIELD, L.G. 2006. Distribution and dynamics of soil organic matter in an Antarctic dry valley. *Soil Biology and Biochemistry*, **38**, 3095–3106.
- ELLIOT, D. & FLEMING, T. 2004. Occurrence and dispersal of magmas in the Jurassic Ferrar Large Igneous Province, Antarctica. *Gondwana Research*, 7, 223–237.
- ETTL, H. & GÄRTNER, G. 1995. Syllabus der Boden-, Luft- und Flechtenalgen. Stuttgart: Gustav Fischer, 729 pp.
- FENICE, M., SELBMANN, L., ZUCCONI, L. & ONOFRI, S. 1997. Production of extracellular enzymes by Antarctic fungal strains. *Polar Biology*, 17, 275–280.
- GREEN, T.G.A. & BROADY, P.A. 2001. Biological soil crusts of Antarctica. In BELNAP, J. & LANGE, O.L., eds. Biological soil crusts: structure, function and management (Ecological Studies, 150). Berlin: Springer, 133–141.
- GREEN, T.G.A., SANCHO, L.G., PINTADO, A. & SCHROETER, B. 2011. Functional and spatial pressures on terrestrial vegetation in Antarctica forced by global warming. *Polar Biology*, **34**, 1643–1656.
- GREGORICH, E.G., HOPKINS, D.W., ELBERLING, B., SPARROW, A.D., NOVIS, P., GREENFIELD, L.G. & ROCHETTE, P. 2006. Emission of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O from lakeshore soils in an Antarctic dry valley. *Soil Biology and Biochemistry*, **38**, 3120–3129.
- HOPKINS, D.W., SPARROW, A.D., GREGORICH, E.G., ELBERLING, B., NOVIS, P., FRASER, F., SCRIMGEOUR, C., DENNIS, P.G., MEIER-AUGENSTEIN, W. & GREENFIELD, L.G. 2009. Isotopic evidence for the provenance and turnover of organic carbon by soil microorganisms in the Antarctic dry valleys. *Environmental Microbiology*, **11**, 597–608.
- HOROWITZ, N.H., CAMERON, R.E. & HUBBARD, J.S. 1972. Microbiology of the Dry Valleys of Antarctica. *Science*, **176**, 242–245.
- KOMÁREK, J. & ANAGNOSTIDIS, K. 1999. Cyanoprokaryota. Teil 1: Chroococcales. In ETTL, H., GÄRTNER, G., HEYNIG, H. & MOLLENHAUER, D., eds. Süßwasserflora von Mitteleuropa. Jena: Gustav Fischer, 548 pp.

- KOMÁREK, J. & ANAGNOSTIDIS, K. 2005. Cyanoprokaryota. Teil 2: Oscillatoriales. In BÜDEL, B., GÄRTNER, G., KRIENITZ, L. & SCHAGERL, D., eds. Süßwasserflora von Mitteleuropa. München: Elsevier, 759 pp.
- LANGE, O.L., MEYER, A. & BÜDEL, B. 1994. Net-photosynthesis of a desiccated cyanobacterium without liquid water in high air humidity alone. Experiments with *Microcoelus sociatus* isolated from a desert soil crust. *Functional Ecology*, 8, 52–57.
- LONGTON, R.E. 1973. Classification of terrestrial vegetation near McMurdo Sound, continental Antarctica. *Canadian Journal of Botany*, **51**, 2339–2346.
- MAGALHÃES, C., STEVENS, M.I., CARY, S.C., BALL, B.A., STOREY, B.C., WALL, D.H., TÜRK, R. & RUPRECHT, U. 2012. At limits of life: multidisciplinary insights reveal environmental constraints in biotic diversity in continental Antarctica. *PLOS One*, 7, 1–10.
- NIENOW, J.A. & FRIEDMANN, E.I. 1993. Terrestrial lithophytic (rock) communities. *In* FRIEDMANN, E.I., *ed. Antarctic microbiology*. New York: Wiley-Liss, 343–412.
- OCHYRA, R., LEWIS-SMITH, R.I. & BEDNAREK-OCHYRA, H. 2008. The illustrated moss flora of Antarctica. Cambridge: Cambridge University Press, 704 pp.
- ØVSTEDAL, D.O. & SMITH, R.I.L. 2001. Lichens of Antarctica and South Georgia. A guide to their identification and ecology. Cambridge: Cambridge University Press, 411 pp.
- PÉREZ-ORTEGA, S., ORTIZ-ÁLVAREZ, R., GREEN, T.G.A. & DE LOS RIOS, A. 2012. Lichen myco- and photobiont diversity and their relationships at the edge of live (McMurdo Dry Valleys, Antarctica). *FEMS Microbial Ecology*, **82**, 429–448.
- POINTING, S.B. & BELNAP, J. 2012. Microbial colonization and controls in dryland systems. *Nature Reviews Microbiology*, 10, 551–562.
- RUPRECHT, U., LUMBSCH, H., BRUNAUER, G., GREEN, T.G.A. & TÜRK, R. 2010. Diversity of *Lecidea* (Lecideaceae, Ascomycota) species revealed by molecular data and morphological characters. *Antarctic Science*, 22, 727–741.
- SCHWARZ, A.M.J., GREEN, T.G.A. & SEPPELT, R.D. 1992. Terrestrial vegetation at Canada Glacier, southern Victoria Land, Antarctica. *Polar Biology*, **12**, 397–404.
- SCHWARZ, A.M.J., GREEN, J.D., GREEN, T.G.A. & SEPPELT, R.D. 1993. Invertebrates associated with moss communities at Canada Glacier, southern Victoria Land, Antarctica. *Polar Biology*, 13, 157–162.
- SEPPELT, R.D., TÜRK, R., GREEN, T.G.A., MOSER, G., PANNEWITZ, S., SANCHO, L.G. & SCHROETER, B. 2010. Lichen and moss communities of Botany Bay, Granite Harbour, Ross Sea, Antarctica. *Antarctic Science*, 22, 691–702.
- SØCHTING, U. & CASTELLO, M. 2012. The polar lichens *Caloplaca darbishirei* and *C. citrina* highlight the direction of bipolar migration. *Polar Biology*, 35, 1143–1149.
- STEWART, K.J., LAMB, E.G., COXSON, D.S. & SICILIANO, S.D. 2011. Bryophyte-cyanobacterial associations as a key factor in N<sub>2</sub>-fixation across the Canadian Arctic. *Plant Soil*, **344**, 335–346.
- STOREY, B.C., FINK, D., HOOD, D., JOY, K., SHULMEISTER, J., RIGER-KUSK, M. & STEVENS, M.I. 2010. Cosmogenic nuclide exposure age constraints on the glacial history of the Lake Wellman area, Darwin Mountains, Antarctica. *Antarctic Science*, 22, 603–618.
- WARREN-RHODES, K.A., RHODES, K.L., POINTING, S.B., EWING, S.A., LACAP, D.C., GOMEZ-SILVA, B., AMUNDSON, R., FRIEDMANN, E.I. & MCKAY, C.P. 2006. Hypolithic cyanobacteria, dry limit of photosynthesis, and microbial ecology in the hyperarid Atacama Desert. *Microbial Ecology*, **52**, 389–398.
- WEBSTER-BROWN, J., GALL, M., GIBSON, J., WOOD, S. & HAWES, I. 2010. The biochemistry of melt water habitats in the Darwin Glacier region (80°S), Victoria Land, Antarctica. *Antarctic Science*, **22**, 646–661.