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Alpine biological soil crusts on the Hochtor (Grossglockner high alpine route, Hohe Tauern, Austria): soils, function and biodiversity

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The Plattenkar, to the east of the Hochtor in the Hohe Tauern, is characterized by numerous karstic forms and by large areas of biological soil crusts (BSCs). BSCs were investigated in a comparative approach as a part of the international SCIN-project. The present study describes the predominant soil types (on fine weathered Rauwacke), compares the chemical and physical characteristics of BSC and underlying soil, and discusses the effects of BSCs on the composition of vascular plants. The most important factors characterizing the soil types in the study area are the BSC layer (composed primarily of microorganisms and lichens), eolian deposits, hydromorphic processes, and slides that lead to buried horizons. Finally, a new soil type "Biogene Krusten-Rendzina" is proposed. We also provide an overview of vascular plants, bryophytes and lichens that cover the BSC layer. The predominant phyla of bacteria and microfungi are presented for the first time from alpine BSCs on the Hochtor, and their ecosystem services such as nitrogen fixation and dissimilatory Fe(III) reduction are addressed.

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Das Plattenkar, östlich vom Hochtor in den Hohen Tauern, fällt durch zahlreiche Karstformen und durch großflächige biologische Bodenkrusten auf. Letztere werden im Rahmen eines internationalen Projektes (SCIN) vergleichend erforscht. In der vorliegenden Arbeit werden die vorherrschenden Bodentypen (aus Rauwacke) systematisch beschrieben, die chemisch-physikalischen Kennwerte von Kruste und Unterboden gegenübergestellt und die Auswirkungen von biologischen Bodenkrusten auf höhere Pflanzen diskutiert. Zu den besonderen bodenbildenden Merkmalen im Gebiet zählen die Krustenauflage (bestehend hauptsächlich aus Mikroorganismen und Flechten), mineralische Staubablagerungen, hydromorphe Merkmale und Überschüttungen (begrabene Horizonte). Als neuer Bodentyp wird die „Biogene Krusten-Rendzina" eingeführt. In tabellarischen Übersichten werden die wichtigsten Gefäßpflanzen, Moose und Flechten, die mit den biologischen Krusten assoziiert sind, dargestellt und kommentiert. Ebenso werden die vorherrschenden Stämme von Bakterien und Mikropilzen erstmals für alpine Bodenkrusten am Hochtor vorgestellt und deren ökosystemare Bedeutung kurz erläutert.

Keywords: Soil types, soil characteristics, Biogene Krusten-Rendzina, vascular plants, bryophytes, lichens, bacteria, microfungi.

Introduction

Hochtor is to be found at the highest point of the Grossglockner high alpine route at an altitude of 2,575 m, and is a historic passage between the Seidlwinkl Valley in Salzburg and the Möll Valley in Carinthia (Hütter 2014). Geologically, the eastern ridge area belongs to the Seidlwinkl Triassic –the largest and richest Triassic layer in the Tauern window. Carbonate rock layers and solution processes have resulted in an intensive karstification that is unexpected in the Hohe Tauern (Fink 1984, Nationalpark Hohe Tauern & Österreichischer Alpenverein 2000, Krainer 2005, Peer et al. 2011). With the appearance of biological soil crusts (BSCs) on the Hochtor, this area is getting more and more attention from scientists, focusing on ecological roles and functions of BSCs in high alpine environments (Huber et al. 2007, Peer 2009, Peer et al. 2010). It was the first time that such comprehensive approach has been applied in the Alps.

Biological soil crusts (also called microbiotic, microphytic or cryptogamic crusts) are assemblages of cyanobacteria, heterotrophic bacteria, green algae, bryophytes, fungi and lichens. Lichen rhizines and bryophytes rhizoids, fungal hyphae, filamentous cyanobacteria, colonies of green algae and their exopolysaccharides form networks in BSCs and aggregate soil particles together (Belnap & Lange 2003, Büdel 2002, 2003, 2005, Concostrina-Zubiri et al. 2014). BSCs contribute to a variety of ecological functions, including soil stabilization, nitrogen fixation, nutrient availability, and vascular plants establishment (e.g. Belnap & Gardner 1993, Eldridge & Greene 1994, Gold et al. 2001, Belnap et al. 2003, Eldridge & Leys 2003, Huber et al. 2007). Together with their binding capacity, they improve aggregate stability and protect underlying soil from erosion. Even though the microbial diversity of the soil and services provided by soil biota are of vital importance for intact ecosystem function, diversity and function of soil microorganisms are rarely studied in the context of conservation planning (Parker 2010).

The important role of BSCs in alpine regions has been more or less neglected in contrast to numerous studies on arid lands, and comparatively few studies have been carried out until today (e.g. Pérez 1997, Gold et al. 2001, Türk & Gärtner 2003). For instance, Pèrez (1997) focused his studies on physical effects of microbiotic crusts in an equatorial high Andean location. The functional influences of cryptobiotic surface crusts in an alpine tundra basin of the Olympic Mountains (Washington, USA), have been treated by Gold et al. (2001). Moreover, Türk & Gärtner (2003) provided an overview of crust communities over carbonate and acid soils of the Alps.

Since 2011, BSCs have become a part of the pan-European research initiative BiodivERsA that offers innovative opportunities for the conservation and sustainable management of biodiversity (http://www.biodiversa.org/). The biodiversity, metabolic activity of BSCs, soil properties and hydrology, as well as the adaption of lichens to various climatic conditions are investigated in this project (Soil Crust International – SCIN, http://www.soil-crust-international.org/), by comparison of BSCs in Öland (Sweden), Gössenheim (Germany), Almería (Spain) and Hochtor (Austria). In addition, the recovery processes of BSCs after disturbance have also been surveyed (Büdel et al. 2014). Our present study focuses on the Hochtor and aims to answer the following questions: i) What are the associated soil types with BSCs on the Hochtor? ii) How do BSCs affect physical-chemical properties of soils? iii) How do BSCs influence composition of higher plants?

Material and Methods

Study area:

The study area is located on the Hochtor/Plattenkar, along the 'Klagenfurter Jubiläumsweg' from the Tauernkopf (2,628 m) to the Rossscharte (2,665 m) (47°4'57"N, 12°51'1"E), and is a part of the Hohe Tauern National Park (Fig. 1). The climate is high alpine with an annual average temperature of -3°C and annual precipitation of about 2,000 mm. From November to June the study area is covered by a thick layer of snow (Auer et al. 2002). The most common rocks in the Seidlwinkl formation are limestone and dolomite marble, as well as gypsiferous dolomite (Rauwacke) (Exner 1964, Krainer 2005). Strong winds and airborne deposits are typical in the area studied, for example, Gruber (1980) calculated an amount of 1,259 kg/ha/a on the north face of the Hochtor, on the basis of sediment material found on the snow fields. The vegetation consists mainly of alpine calcareous grasslands, cushion plants and scree plants (Hartl & Peer 2005).

Sampling and soil analysis:

From 2005 to 2013, 20 soil profiles were described at various sites on the Plattenkar. In total, an area of about 1 ha was investigated. The soil types were classified according to the Austrian Soil Systematics (Nestroy et al. 2011) and the World Reference Base for Soil Resources (WRB 2006), respectively. Identification of soil color refers to Munsell Standard Soil Color Charts (Munsell 1970). Both BSC material and underlying soils, separated by a spatula, were collected from 10 to 40 sites. The buried horizon has been provisionally sampled only once. All BSC and underlying soil samples were air-dried, passed through a 2 mm-sieve or ground, and then analyzed by using standard methods. The following parameters were analyzed: 1) pH in 1:2.5 soil-$CaCl_2$ suspensions according to ÖNORM L 1083 (1989), 2) electrical conductivity (EC) in 1:5 soil-water suspensions (Visconti et al. 2010), 3) particle size distribution by sieve and pipette method according to ÖNORM L 1061 (1988), 4) water holding capacity by gravimetric measurement after soil saturation with water and drying at 105°C on cylinder samples including BSC and underlying soil (Wilke 2005), 5) aggregate stability by wet sieving method (Foster 2011), 6) carbonate content by Scheibler–calcimeter according to ÖNORM L 1084 (1989), 7) plant-available P according to CAL-Method by Schüller (1969), 8) exchangeable K, Ca, and Mg in $BaCl_2$ extraction solution according to Blum et al. (1996), 9) total concentrations of Fe, Mn, K, Ca and Mg in nitric acid (HNO_3) and perchloric acid ($HClO_4$) according to Blum et al. (1996), 10) total N and organic C by Elemental Analyzer (EA 1110, CE Instruments) at the University of Vienna.

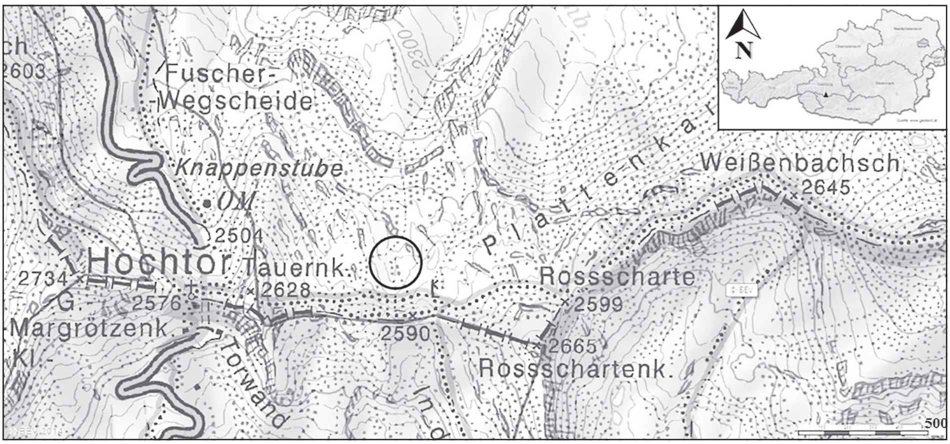

Fig. 1: Map of Hochtor/Plattenkar and location of study area (framed) Scale: 1:25,000. Sources: http://www.austrianmap.at/amap/index.php?SKN=1&XPX=637&YPX=492; http://www.geoland.at. – Abb. 1: Untersuchungsgebiet und Lage der Versuchsfläche (Kreis) am Hochtor/Plattenkar. Maßstab: 1:25.000. Quellen: http://www.austrianmap.at/amap/index.php?SKN=1&XPX=637&YPX=492; http://www.geoland.at.

Plant identification:

The coverage of vascular plants and BSCs was calculated by a 25 x 25 cm frame which was set on 150 randomly selected plots in the study area. The taxon identification and nomenclature follows Fischer et al. (2005) for vascular plants and Frey et al. (1995) and Grims (1999) for bryophytes. For lichen identification, references of Poelt (1969), Poelt & Vězda (1977, 1981), and Wirth et al. (2013) were used. The nomenclature corresponds to Poelt (1969), Türk & Hafellner (2010), and Wirth et al. (2013).

Bacterial and fungal diversity determination:

For details on sampling, DNA extraction, pyrosequencing and data processing to assess prokaryotic community structure see Maier et al. (2014). ITS1F and ITS2 primer pair (Anderson & Cairney 2004) was used to determine the diversity of fungi. To process the fungal data Acacia v1.52 and BLAT analysis pipeline of the web server SnoWMan (https://snowman.genome.tugraz.at/snowman/index.jsp) were used.

Statistical analysis:

Differences in soil properties between BSC and underlying soil were investigated by either applying one-way ANOVA or by using the non-parametric Kruskal-Wallis test, if assumptions for parametric tests could not be met. The significance level (alpha) was set at $p < 0.05$. All statistical analysis were performed with IBM SPSS (Version 22).

Results

Soil classification

The topography and intense postglacial morphodynamics on the Hochtor caused various soil types in terms of profile depth and profile structure. The most common soil types and their characteristics are described in Table 1.

Tab. 1: Soil types and horizon sequences of selected soils on the Hochtor/Plattenkar. – Tab. 1: Bodentypen und Profilaufbau ausgewählter Böden am Hochtor/Plattenkar.

Soil type (Austrian Soil Systematics)	Soil type (WRB)	Horizon sequence	Soil depth in cm	Parent material
Carbonathaltiger Grob- und Feinmaterial Rohboden	Skeletic Regosol	A_iC_h-C_v	0–3	Coarse to fine scree material of Dolomite marble and sandy-gritty weathered Rauwacke
Proto-Rendzina	Rendzic Regosol	(K_{bio})-A_{hi}-C_{v1}-C_{v2}	1–10	Coarse to fine scree material of Dolomite marble and sandy-gritty weathered Rauwacke
Biogene Krusten-Rendzina, tw. vergleyt	Rendzic (stagnic) Regosol	K_{bio}-$A_{hi,\ eg}$-C_{v1}-C_{v2}	15–20/25	Sandy-gritty weathered Rauwacke
Überlagerte tw. vergleyte biogene Krusten-Rendzina	Colluvic (stagnic) rendzic Regosol	K_{bio}-$AC_{hi,\ eg}$-$B_{beg,\ g}$-C_{v1}-C_{v2} (type I) K_{bio}-A_{hi}-C_{v1}-$B_{beg,\ g}$-C_{v2}-C_{v3} (type II)	20–25/30	Sandy-gritty weathered Rauwacke

Microorganisms such as Cyanophyta and Chlorophyta as well as traces of fine organic matter have already been found in the loose scree. They are carried by wind and washed into debris and sandy-gritty weathered Rauwacke by rain and melt water. These components make the top soil a little darker (10 YR 6/1–6/2) in contrast to the sandy-gritty parent material of Rauwacke which is almost white due to the abundance of gypsum (10 YR 6/2 and 10 YR 8/3). The soil texture varies from medium silty sand (Su3) to highly silty sand (Su4), with more fine silt and clay in deeper layers. The pH values range between 7.4 and 7.8 (Huber et al. 2007). The scree is superficially compacted by snow and wind pressure. Debris and rock strips are recognizable in some places. The amount of larger separates is over 40 %; therefore, the soil type is classified as "Carbonathaltiger Grob- und Feinmaterial Rohboden" (Austrian Soil Systematics) or Skeletic Regosol (WRB Systematics). Through successive plant colonization, decomposition, humus formation, and sedimentation of mineral dust, an initially very thin, near-black but mineral-rich BSC-layer with small lichen thalli, green algae and cyanobacteria is developed (7.5 YR 2/2–3/1). In this soil, litter is generally absent, whereas grey-brown infiltration of humus substances is visible beneath the BSC, reaching a depth of 10–15 cm (A_{hi}, 10 YR 4/2). The parent material exhibits different colored strata depending on the amount of gypsum: light brown, yellowish or pink (10 YR 6/4, 10 YR 8/4, 7.5 YR 8/3). Owing to the pronounced organismic (humus) layer, we denote this soil type as "Proto-Rendzina" or "Rendzic Regosol". Without disturbance, a pinnacled black BSC layer (7.5 YR 2/1–3/1) of 0.2–1cm height is developed which can be more or less easily lifted from the underlying soil. On the BSC-layer, lichens, bryophytes as well as some cushion plants (e.g. *Silene acaulis s. l.*, *Minuartia sedoides*, *Saxifraga rudolphiana*) are settled. There are a lot of airborne dusts within the cushion plants. Within the BSC, the soil texture is classified as a very silty sand (Su4), and the underlying soil is coarser, belonging to a medium and slight silty sand (Su3, Su2), respectively. The organic matter content of the BSC is at 1–6 % by weight, it is to be considered rather low compared to typical alpine Rendzinas. However, coprogenic amounts of invertebrates could not be detected so far (cf. Franz 1943, 1945, 1969, Haybach 1971/72, 1992). The BSC matrix on the Hochtor site may consist mainly of microorganism assemblages.

A horizon specification for such a special BSC layer has not been described in the Austrian Soil Systematics. Therefore, we denote this horizon temporarily as 'K_{bio}' (biogene Kruste). The underlying illuvial horizon (A_{hi}) is wavy delimited, 10–15cm thick and much brighter than the dark BSC layer above (10YR 5/3–5/4). If it is hydromorphically influenced, the color is flecked with gray and gray-brown (A_{eg}: 7.5 YR 4/1 and 7.5 YR 5/4–4/6). The BSC and underlying soil have pH values of 7.3 and 7.4, respectively. The parent material is again sandy-gritty weathered Rauwacke and shows different colored strata. We propose this more mature soil type as "Biogene Krusten-Rendzina, teilweise vergleyt" or Rendzic (stagnic) Regosol. It is notable that dark horizontal layers have been occasionally formed in different soil depths. They display a laminated structure, partly displaced and interrupted with mosaic-like dark brown (7.5 YR 2/2) and rust-brown aggregates (5 YR 3/4). The colors of the aggregates may have been intensified by waterlogging after the snow melt. In addition, glittering mineral granulates composed of quartz and white mica are interspersed in the dark horizontal layers, probably originating from surrounding mountain tops (e.g. Tauernkopf, Rossscharten Kopf) that belong to the Brennkogel formation and overlay the Seidlwinkl Triassic. The dark horizon directly underneath the AC_{hi}/AC_{eg}-horizon is sharply differentiated from the underlying Rauwacke grus (Fig. 2, type I). The deeper buried horizon at 10 to 20 cm is over- and underlaid by Rauwacke grus and sometimes also gleyic

($B_{beg, g}$). The C-horizon is fine weathered Rauwacke, with colors from almost pure white to light brown, reddish brown and pink. Similar to the soil type as described above, this soil type we denote as "Kolluviale, tw. vergleyte biogene Krusten-Rendzina" or Colluvic rendzic (stagnic) Regosol (Fig. 2, type II). Buried horizons are particularly frequent on the base of hillslopes where the upper part is denudated through downslope soil movement.

The mineral composition of BSC, underlying soil and buried horizon was exemplary examined under the microscope of 600x magnification. All grains (> 0.125 mm) were angular and subangular formed, mainly composed of quartz, white mica and calcite. Additionally, typical for the BSC layer and the buried horizon were limonitic ore incrustations of various fine-grained Fe- and Mn-hydroxides (> 60 % in BSC layer, and > 80 % in buried horizon).

Soil characteristics

The analysis of nutrients in BSCs showed low contents of N, P and K, but high contents of Ca and Mg (Tab. 2). In comparison with underlying soil, the plant available P and K were 2–3 times higher in BSC, whereas no great differences of Ca and Mg were seen between BSC and underlying soil. However, total N and total organic C were remarkably higher in BSC than in underlying soil. The other elements (Fe, Mn, Mg, Ca and K) were at similar levels between BSC and underlying soil. Higher contents of clay and humus were observed in BSC, therefore the aggregate stability was increased, and the soil erosion was reduced (HUBER et al. 2007). Consequently, in sites where the BSC layer is destroyed, denudation and erosion gullies on the bare soil became evident.

As described in Tab. 2, the buried dark horizon exhibited significantly higher values of plant available Ca and Mg, compared to the other soil horizons. However, the total contents of

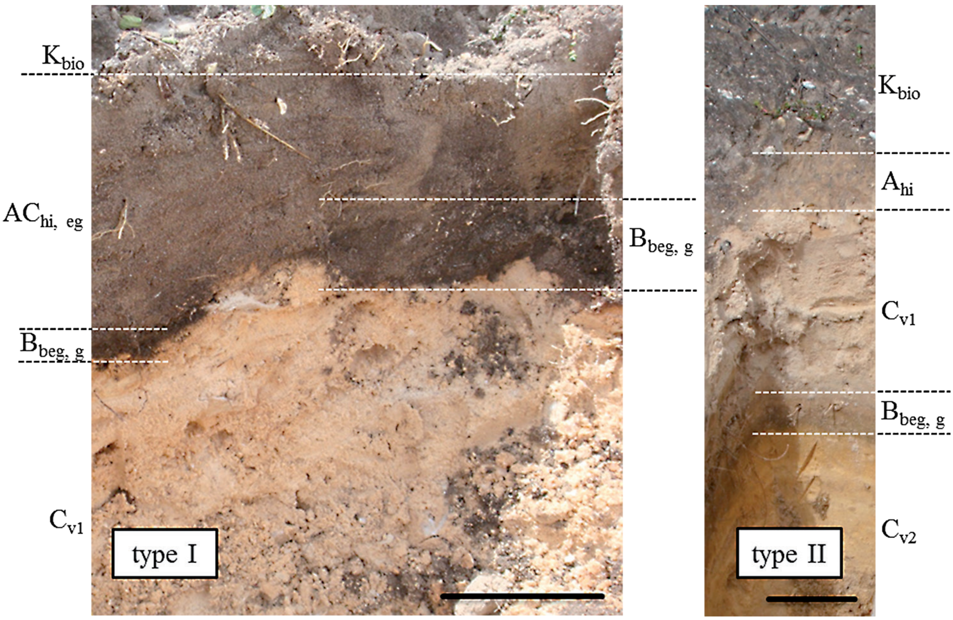

Fig. 2: Colluvic (stagnic) rendzic Regosol, type I and II, measuring bar: 5 cm. – Abb. 2: Überlagerte, tw. vergleyte biogene Krusten-Rendzina, Typ I und II, Messbalken: 5 cm.

Tab. 2: Physical-chemical properties in crust layer, underlying soil and buried horizon on the Hochtor/Plattenkar (Mean values and standard deviation; n = 10–40 for crust and underlying soil, 1–3 for buried horizon). – Tab. 2: Physikalisch-chemische Kennwerte in der Krustenauflage, im Unterboden und im begrabenen Horizont am Hochtor/Plattenkar (Mittelwerte und Standardabweichung; n = 10–40 für Kruste und Unterboden, 1–3 für begrabenen Horizont).

Parameters	BSC	underlying soil	buried horizon
sand (%)	58±6	57.7±9	67.2±0.7
coarse silt (%)	34.4±7.5	34.7±10	16.2±1.1
fine silt (%)	4.8±1.7	5.8±2.4	13.3±1
clay (%)	2.8±1.5*	1.8±1	3.3±0.9
water holding capacity (g/100g DW)	48.1±24		–
aggregate stability (%)	15.3±7.7	8.9±8.7	–
pH	7.34±0.05*	7.43±0.09	7.3
EC (µs/cm)	169±34*	88±15	87.5
available P (mg/100g)	0.5±0.3*	0.2±0.1	0.078
available Ca (mg/100g)	211.8±111*	171.4±137.2	578
available Mg (mg/100g)	34.8±20.8*	29.5±25.3	88.24
available K (mg/100g)	2.9±1.5*	0.8±0.6	0.97
Total Ca (%)	14.3±4.9	15.9±3.2	1.7±0.1
Total Mg (%)	9.2±2.9	10.8±2.7	1.7±0.04
Total K (%)	0.07±0.04	0.06±0.06	0.13±0.003
Total Fe (%)	1.46±1.1	1.46±0.6	4.65±0.3
Total Mn (%)	0.08±0.04	0.07±0.04	0.25±0.007
Ntot (%)	0.18±0.13	0.08±0.04	–
TC (%)	6.6±6	2.5±1.6	9.9±0.4
TOC (%)	2.12±1.6	0.97±0.5	–
$CaCO_3$ (%)	3.1±2.3	3.8±2.2	0.2

* $p < 0.05$ (parameters that contain over 20 samples were statistically tested.)

Ca and Mg were lower. Total Fe and total Mn were up to 4 times higher in the buried horizon as compared to the other soil horizons, and total C was 1.5 times higher compared to the BSC. The pH value was around 7.3 and not different to the other soil horizons. EC was similar to the underlying soil but about half as much as BSC. Particle size distribution analysis clearly showed more fine silt and clay and a little more sand compared to other soil horizons (Su3). The carbonate determination by Scheibler partly exhibited differences by more than twice in the same sample, depending on the proportion of Ca-carbonate and Mg-carbonate. However, many other parameters also exhibited a remarkably wide variation (see SD in Tab. 2), indicating high inhomogeneity of the material which could be caused both by sampling procedure –a contamination of the BSC with mineral particles from the underlying soil could not be completely excluded –and by the alternation of surface composition with more or less lichen thalli, plant residuals, stones and other dust particles over a short distance. Furthermore, terrain factors like inclination and exposition are often different from plot to plot.

Species composition

Over several years all relevant plants have been recorded, whereas plant compositions differ from year to year due to changing environmental conditions and life cycle which regulates the growth of plants. Furthermore, through more refined methods new taxa were found (e.g. lichens). The given lists in Tab. 3 include all records from the last two years and represent also the current situation. For specimen records only crusted parts were selected.

Tab. 3: Lichens on BSCs on the Hochtor/Plattenkar according to their growth form and the substratum. Common species are underlined. – Tab. 3: Flechten auf biologischen Krusten am Hochtor/Plattenkar, differenziert nach Wuchsform und Substrat. Besonders häufig auftretende Arten sind unterstrichen.

I. Real crustose, placodioid and squamulose terricolous lichens

Bilimbia lobulata (Sommerf.) Hafellner & Coppins, syn.: *Myxobilimbia l.* (Sommerf.) Hafellner
Bilimbia microcarpa Th. Fr., syn.: *Myxobilimbia m.* (Th. Fr.) Hafellner
Buellia elegans Poelt
Buellia epigaea (Pers.) Tuck.
Catapyrenium cinereum (Pers.) Körb.
Gyalecta foveolaris (Ach.) Schaer.
Fulgensia bracteata (Hoffm.) Räsänen subsp. *deformis* (Erichsen) Poelt
Lecidea berengeriana (A. Massal.) Nyl., syn.: *Mycobilimbia b.* (A. Massal.) Hafellner & Wirth
Phaeorrhiza nimbosa (Fr.) H. Mayrhofer & Poelt
Placidium lachneum (Ach.) B. de Lesd.
Placynthiella oligotropha (J. R. Laundon) Coppins & P. James
Polyblastia sendtneri Kremp.
Protoblastenia terricola (Anzi) Lynge, syn.: *P. siebenhaariana* (Körb.) J. Steiner var. *terricola* (Anzi) Hafellner & Türk
Psora decipiens (Hedw.) Hoffm.
Rinodina roscida (Sommerf.) Arnold
Squamarina gypsacea (Sm.) Poelt
Tetramelas papillatus (Sommerf.) Kalb, syn.: *Buellia p.* (Sommerf.) Tuck.
Toninia diffracta (A. Massal.) Zahlbr.
Toninia opuntioides (Vill.) Timdal
Toniniopsis obscura Frey. According to BÜDEL et al. (2014) this species has been misinterpreted until now and may occur only occasionally in biological crust on the Hochtor/Plattenkar.

II. Crustose lichens growing on mosses and plant remains

Caloplaca ammiospila (Wahlenb.) H. Olivier
Caloplaca sinapisperma (Lam. & DC.) Maheu & Gillet
Caloplaca stillicidiorum (Vahl) Lynge, syn.: *C. cerina* var. *muscorum* (A. Massal.) Jatta
Candelariella aurella (Hoffm.) Zahlbr.
Lecanora epibryon (Ach.) Ach.
Lecanora hagenii (Ach.) Ach. var. *fallax* Hepp
Lecidea hypnorum Libert, syn.: *Mycobilimbia h.* (Libert) Kalb & Hafellner
Lecidella wulfenii (Hepp) Körb.
Megaspora verrucosa (Ach.) Hafellner & Wirth
Ochrolechia upsaliensis (L.) A. Massal.
Varicellaria rhodocarpa (Körb.) Th. Fr.

III. Foliose, terricolous lichens

Collema tenax (Sw.) Ach. em. Degel.
Hypogymnia physodes (L.) Nyl. on soil!
Leptogium cf. *tetrasporum* Th. Fr.
Lobaria linita (Ach.) Rabenh.

Tab. 3, Fortsetzung

Peltigera rufescens (Weiss) Humb.
Physconia muscigena (Ach.) Poelt
Solorina bispora Nyl. var. *bispora*
Solorina saccata (L.) Ach.

IV. Fruticose terricolous lichens

Alectoria ochroleuca (Hoffm.) A. Massal.
Allocetraria madreporiformis (Ach.) Kärnefelt & Thell, syn.: *Dactylina m.* (Ach.) Tuck.
Bryoria chalybeiformis (L.) Brodo & D. Hawksw.
Cetraria islandica (L.) Ach.
Cetraria muricata (Ach.) Eckfeldt
Cladonia macroceras (Delise) Hav.
Cladonia pyxidata (L.) Hoffm. subsp. *pyxidata*
Cladonia symphycarpia (Flörke) Fr.
Dactylina ramulosa (Hook. f.) Tuck.
Evernia divaricata (L.) Ach.
Flavocetraria cucullata (Bellardi) Kärnefelt & A. Thell
Gowardia nigricans Halonen, Myllys, Velmala & Hyvärinen, syn.: *Alectoria n.* (Ach.) Nyl.
Thamnolia vermicularis (Sw.) Ach. ex Schaer. var. *vermicularis*
Vulpicida tubulosus (Schaer.) J. E. Mattsson & M. J. Lai

Parasitic fungus on *Caloplaca sinapisperma*: *Arthopyrenia bryospila* (Nyl.) Arnold

The cover degree of the BSCs within the 150 plots reaches 10 % to 40 %, depending on the proportion of stones and vegetation (Fig. 3). The predominating dark colour suggests a high proportion of cyanobacteria, e.g. *Nostoc*, *Oscillatoria*, *Chroococcus*, *Gloeocapsa* (Büdel et al. 2014). Proteobacteria, Actinobacteria, Acidobacteria, and Bacteroidetes were dominant in BSCs and underlying soil. In addition, phyla including Verrucomicrobia, Planctomycetes, Chloroflexi, Gemmatimonadetes, Armatimonadetes, Nitrospira and Firmicutes were also present. Archaeal sequences (Crenarchaeota) were relatively rare (0.7 % of reads). Alphaproteobacteria (order Rhizobiales), Actinobacteria (order Actinomycetales), Betaproteobacteria (order Burkholderiales) and Sphingobacteria (order Sphingobacteriales) contributed mainly to the bacterial community of the BSC and the underlying soil. The classes Acidobacteria_Gp16, Acidobacteria_Gp17 and Acidobacteria_Gp7 were overrepresented, and Acidobacteria_Gp3, Sphingobacteria, Cyanobacteria and Alphaproteobacteria were underrepresented in the underlying soil samples when compared to BSC samples. In all, 16 % of the sequences could not be assigned to known bacterial or archaeal phyla. The relative contribution of fungal classes to the overall diversity of the study location is shown in Figure 4.

On the Plattenkar, 53 lichen species have been found so far (Tab. 3), and cover 0.1 % to 50 % of BSCs, depending on successional stage and stability of BSC and environment conditions. Most of them prefer calcareous soil or bryophytes and plant remains over basic substratum. They are predominantly common species in the Limestone Alps; however they occur also in Central Alps when carbonate is present. On BSCs, crustose, placodioid and squamulose terricolous species like *Bilimbia lobulata*, *Buellia elegans*, *Catapyrenium cinereum*, *Fulgensia bracteata* subsp. *deformis*, *Lecidea berengeriana*, and *Psora decipiens* are common. Bryophytes and plant remains enable the growth of the other crustose lichens over calcareous soil. Foliose and fruticose lichens are relatively rare, only *Peltigera rufescens*, *Solorina bispora*, and *S. saccata* exhibit a higher frequency. *Collema tenax* and *Peltigera-rufe-*

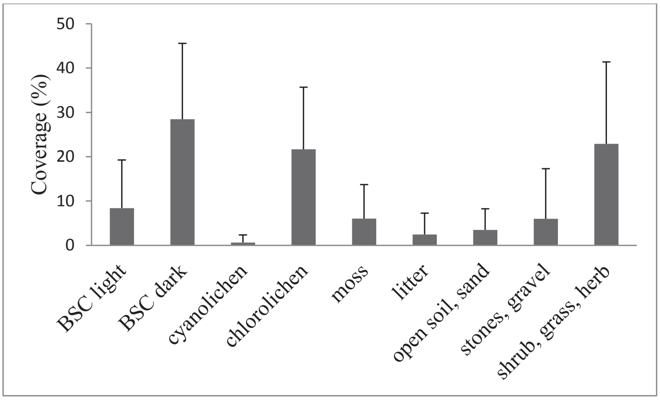

Fig. 3: Coverage degree of components within biological soil crusts on the Hochtor (graph shows mean values and standard deviation). – Abb. 3: Zusammensetzung der biologischen Bodenkrusten am Hochtor (dargestellt sind die Mittelwerte und die Standardabweichung).

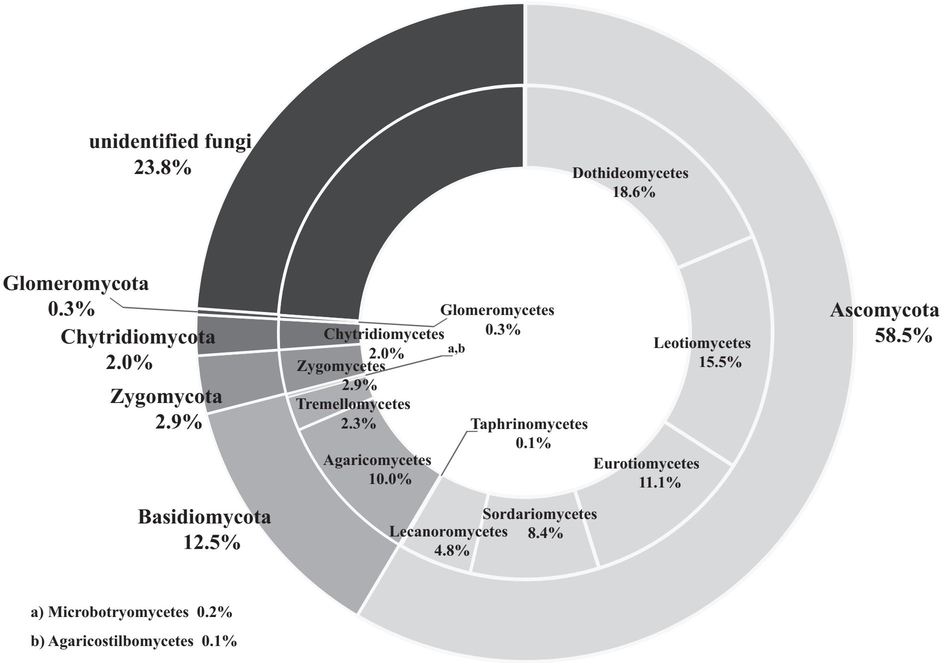

Fig. 4: Relative contribution of fungal classes to the total diversity in biological soil crusts (n = 3). Taxa that could be classified represented five fungal phyla: Ascomycota (58.5 %), Basidiomycota (12.5 %), Zygomycota (2.9 %), Chytridiomycota (2.0 %) and Glomeromycota (0.3 %). The diversity at the site was mainly represented by the following fungal orders: Pleosporales, Helotiales, Chaetothyriales, and Hypocreales (Ascomycota) as well as Thelephorales (Basidiomycota). – Abb. 4: Das Kreisdiagramm zeigt Pilze auf Klassen-Ebene, die zur Diversität in biologischen Bodenkrusten beitragen (n = 3, relative Abundanz). Die folgenden fünf Pilz-Phyla sind vertreten: Ascomycota (58,5 %), Basidiomycota (12,5 %), Zygomycota (2,9 %), Chytridiomycota (2,0 %) and Glomeromycota (0,3 %). Vier Ordnungen der Ascomycota (Pleosporales, Helotiales, Chaetothyriales, Hypocreales) und eine Ordnung der Basidiomycota (Thelephorales) waren hauptsächlich am Standort Hochtor vorzufinden.

scens are cyanobacterial lichens. Moreover, in *Lobaria linita,* the cyanobacterial component is housed in numerous internal cephalodia. Therefore, all these lichens have the potential for nitrogen fixation (Henrikson & Simu 1971). Most of fruticose species grow in communities with higher plants. Remarkably, the lichenicolous fungus *Arthopyrenia bryospila* grows on *Caloplaca sinapisperma*, whose closest relatives are lichenized.

Regarding bryophytes (mosses and liverworts), the cover degree is rather low within the BSC layer (less than 10 %). Twenty-seven species have been recorded (Tab. 4). Bryophytes were often not completely developed due to the severe climate conditions on the Hochtor, it was therefore sometimes difficult to classify them. In high alpine regions, bryophytes commonly reproduce asexually by rhizoid buddings, and the production of spore capsules

Tab. 4: Vascular plants and bryophytes on BSCs on the Hochtor/Plattenkar. – Tab. 4: Gefäßpflanzen und Moose im Bereich der biologischen Bodenkrusten am Hochtor/Plattenkar.

Vascular plants	Bryophytes
Achillea atrata L.	**Mosses**
Arabis caerulea (All.) Haenke	*Bryum argenteum* Hedw.
Braya alpina Sternb. et Hoppe	*Bryum pallens* (Brid.) Sw. in Röhl.
Carex atrata L.	*Bryum spec.*
Carex rupestris All.	*Campylium chrysophyllum* (Brid.) Lange
Cerastium uniflorum Clairv.	*Distichium capillaceum* (Hedw.) BSG
Comastoma nanum (Wulfen) Toyok.	*Distichium inclinatum* (Hedw.) Bruch & Schimp.
Dianthus glacialis DC.	*Ditrichum spec.*
Draba aizoides L.	*Drepanocladus uncinatus* Hedw.
Dryas octopetala L.	*Hypnum bambergeri* Schimp.
Euphrasia salisburgensis Funck ex Hoppe	*Hypnum revolutum* (Mitt.) Lindb.
Festuca pumila Chaix	*Meesia uliginosa* Hedw.
Gentiana bavarica var. subacaulis (Wahlenb.) Schleich.	*Pohlia spec.*
Gentiana orbicularis Schur	*Polytrichum alpinum* (Hedw.) G. L. Sm.
Kobresia myosuroides (Vill.) Fiori	*Polytrichum norvegicum* Hedw.
Minuartia gerardii (Willd.) Hayek	*Pottiaceae* – unknown species
Minuartia sedoides (L.) Hiern	*Racomitrium spec.*
Pedicularis asplenifolia Floerke	*Tayloria froelichiana* Mitten ex Brotherus
Persicaria vivipara (L.) Delarbre	*Tortella tortuosa* (Hedw.) Limpr.
Phyteuma globulariifolium Sternb. & Hoppe	*Tortula norvegica* (F. Weber) Wahlenb. ex Lindb.
Primula minima L.	*Tortula ruralis* (Hedw.) Gaertn., Meyer, & Scherb.
Ranunculus alpestris L.	
Salix herbacea L.	**Liverworts**
Salix serpillifolia Scop.	*Anthelia juratzkana* (Limpr.) Trevis.
Saxifraga androsacea L.	*Blepharostoma trichophyllum* (L.) Dumort.
Saxifraga oppositifolia L.	*Leiocholea spec.*
Saxifraga rudolphiana Hornsch.	*Lophozia spec.*
Sedum atratum L.	*Lophozia sudetica* (Nees ex Huebener) Grolle
Sesleria ovata (Hoppe) A. Kern.	*Riccia breidleri* Jur. ex Steph.
Silene acaulis s. l.	*Scapania cuspiduligera* (Nees) K. Müll.
Veronica alpina L.	
Veronica aphylla L.	

might be suppressed (Meusel 1935). The species *Lophozia sudetica, L. wenzelii*, and *Scapania cuspiduligera* are the most common liverworts, and the species *Bryum argenteum*, *Distichium capillaceum,* and *Meesia uliginosa* are the most common mosses. It should be also mentioned that the species *Tayloria froelichiana* –a member of the rare family Splachnaceae, is typical for a bird eutrophicated site. *Nardia breidleri* is a rare high alpine region species and appears together with *Anthelia juratzkana* in long snow-covered depressions. Species of the large Pottiaceae family could not definitely be assigned on the Hochtor.

Vascular plants cover the BSC surface between 10 % and 40 %. In total, 32 species of vascular plants have been found, of them C*arex atrata*, *Persicaria vivipara*, *Primula minima*, *Ranunculus alpestris*, *Salix herbacea*, *Saxifraga oppositifolia/S. rudolphiana*, *Sesleria ovata,* and *Silene acaulis s.l.* are the most common species (Tab. 4). They are all typical high alpine species, growing in snow-beds and on moist scree. It is remarkable that some species like *Primula minima*, *Salix herbacea*, *Cerastium uniflorum*, and *Minuartia sedoides* are calcifuge plants. The species *Saxifraga rudolphiana* and *Braya alpina* are considered to be endemic (Fischer et al. 2005). Most vascular plants grow in frost cracks within the BSC or well protected behind rocks. Starting from these points they spread over the BSC surface by runners (e.g. *Saxifraga oppositifolia*).

Discussion

Soil types on the Hochtor have been generated by a high variety of geomorphological forms on the Plattenkar, ranging from low developed, skeletal soils and Proto-Rendzinas on exposed ridges, to deep colluvial and alluvial soils at the footslopes and in depressions (Peer 1993, Huber et al. 2007). The latter often exhibit hydromorphic features like grey-pale marbling and rust spots due to influence of waterlogging. Reddish colored soil types like "Kalklehm-Rendzinas" (Cromic Cambisol, Terra fusca) also occur in the study area, mainly on plains and plateaus, and may hint to residual (paleoclimatic) soil development (cf. Kubiena 1948, 1950, Janik & Schiller 1960, Biermayer & Rehfuess 1985, Nestroy et al. 2013). Such soil types are usually covered by a dense alpine meadow. Therefore, they are not dealt with here. In the relevant national and international literature on soil systematics there are no corresponding names for both the BSC layer and the soil type. Consequently, we proposed new terms for both the BSC layer (K_{bio}= biogene Kruste) and the soil type (Biogene Krusten-Rendzina). Referring to the description of Regosol in the WRB-systematics (WRB 2006), this soil type was used in the present study. It is not shallow and stony enough to be Leptosol. The dark buried horizon within the soil profile may result from illuvial effects of humus and Fe- and Mn-oxides/hydroxides, as well as from mineral precipitation. On the surface of BSCs, the polygonal structure of channels scoured out by rain water and melt water can be recognized, in which sand and gravels have been accumulated. Consequently, dark humus solutions from the BSC drains have infiltrated the soil (see Fig. 2, type I). Humus substances may fix Fe (inclusive Mn) in reduced metallic complexes and the crystallization, probably the formation of Fe- and Mn-oxides/hydroxides is prevented. Only when soil becomes dry, Fe- and Mn-oxides can be crystallized (Schwertmann 1964, Blume & Schwertmann 1969, Schwertmann & Taylor 1977). The black to rust-/reddish-brown aggregates ($B_{beg,\,g}$) below the AC_{hi}-horizon could have been formed from these dynamics. Probably the minerals such as quartz and mica also infiltrated along with the melt water and deposited. However, investigations that can give a definite answer are not available so far. Huber et al. (2007) reported that the Fe_o/Fe_d ratio in crust ranges from 0.19 to 0.28, implying relative high amorphous Fe in crust (assuming poorly crystalline goethite with some ferrihydrite, not yet analyzed) which is typical for young and low developed soils (Cornell & Schwertmann 1996). Similar results have also arisen from the Fe_d/Fe_t ratio of 0.17 which suggests a low degree of weathering. A comparable hydrodynamic can also be assumed for the deeper buried horizon observed occasionally on the Plattenkar. The contents of amorphous and pedogenetic Fe are considerably higher in the buried horizon than in crust, and the ratio of Fe_d/Fe_t increases to 0.19. This can be interpreted as a little higher age of the soil horizon. The stratigraphic orientation could be given rise to the reaction of oxide precipitation on a discontinuity of pores, together with a change of structure/texture within the soil profile. The buried horizons in the deeper soil profile are probably correlated with stable phases during postglacial warm periods (^{14}C-datings show ages of 2,200±150 BP and 1,540±135 BP, as found in the Piffkar which has similar soil profiles, Klinge & Lehmkuhl 1998). It can be assumed that eolian dust was also deposited during this period. The buried horizons ($B_{beg,\,g}$) were then solifluidal overlaid in the subsequent cold periods (Heuberger 1968, Patzelt 1972, Veit 1993).

As mentioned above, the entire area is exposed to pronounced eolian influence, evidenced by dark horizons in the snow profile and dirty brown colored snow fields in spring. Together with the short-distance transport of mineral particles, Saharan dusts from the southwest can reach the main ridge of the Alps on a large scale and deposit fine dust several times per year in the lee side of the Alps (http://www.zamg.ac.at/cms/de/aktuell, http://www.sonnblick.net/portal/). In addition, pollen grains, plant and animal residues are also transported by air along with the fine dust (cf. Fritz 1976, Sattler et al. 2010). All these deposits may be stored both on the surface of recent BSCs and in buried horizons. The particle size distribution of dust (generally < 60 µm) and the mineral composition imply long- and short-distance transports. However, based on the preliminarily microscopical determination there were no signs of eolian transport because all grains were angular or subangular formed and had no pitted grain surface. The effect of airborne dust on the soil formation in karst areas of the Northern Limestone Alps and Swiss Alps is addressed in publications of Sticher et al. (1975), Küfmann (2008), and Duffy (2011). In summary, it can be stated that the specific soil features on the Hochtor/Plattenkar are the result of hydromorphic, gelisolifluidal and eolian processes. The BSC which has been interpreted as a dense and compact assemblage of cyanobacteria, heterotrophic bacteria, green algae, bryophytes, fungi and lichens protects the underlying soil not only physically (see the results of aggregate stability) but also provide plant available nutrients, originating from decomposition processes and eolian deposition as well.

It is not yet completely understood why BSCs are so well developed in the high alpine region of the Plattenkar. This is especially remarkable in comparison with the semi-arid and arid ecosystems from which BSCs have been described primarily (e.g. Anderson et al. 1982, West 1990, Eldridge 1993, Belnap & Gardner 1993, Eldridge & Greene 1994, Garcia-Pichel et al. 2001, Yeager et al. 2004, Nagy et al. 2005, Castillo-Monroy et al. 2011, Zhang et al. 2011, Steven et al. 2013). The extraordinary growth of microorganisms might be caused not only by the proper moisture from high precipitation and long period of snow cover, fine sandy-silty parent material, and high pH values, but also by their capability to tolerate high levels of UV radiation and the production of UV protectants, as described in the study of Janatková et al. (2013). The high cover degree of BSCs and the prevalence of cyanobacteria in the study area have also been observed in the alpine zones of the Tibetan Plateau, where approximately 40 % of the soil surface is covered by BSCs. The biomass of phototrophs in BSCs was up to five times higher than in uncrusted soils and the biomass of cyanobacteria tended to increase with increasing elevation (Janatková et al. 2013). Furthermore, cyanobacteria contributed up to 99 % of the biovolume of the photoprohpic communites in Himalayan soils (Reháková et al. 2011).

In Europe, studies have been conducted on the prokaryotic communities of bryophyte and lichen-dominated BSCs (Castillo-Monroy et al. 2011, Moquin et al. 2012, Maier et al. 2014). Bacteria in microbial mats and endolithic communities are usually arranged along vertical gradients (Seckbach & Oren 2010), and similar patterns have also been observed in BSCs. Our results which showed that BSC communities were distinct in compositional character from those in underlying soil samples is in line with the observations of Garcia-Pichel et al. (2003), Steven et al. (2013) and Elliott et al. (2014). Several metabolic strategies such as photosynthesis, nitrogen fixation, ammonia oxidation, and methylotrophy, were reported in the class Alphaproteobacteria (Williams et al. 2007). Studies on Actinobacteria revealed their nitrogen-fixing capacity (Sellstedt & Richau 2013).

The major fungal representatives in BSCs so far observed, are members of the Ascomycota, particularly belonging to the Pleosporales. The Pleosporalean genera *Alternaria, Ulocladium* and *Phoma* were found to be highly abundant and geographically widespread in BSCs (Bates et al. 2010). Our analysis confirms the dominance of Ascomycota, which are primarily represented by the order Pleosporales and Helotiales/Leotiales on the Hochtor. The prevalence of the Pleosporales, characteristically having darkly pigmented hyphae or spores is thought to be due to their ability to endure high temperature, desiccation and shortage of nutrients available at arid regions. Nonetheless, functional analogy of dark septate fungi to mycorrhizal fungi has been suggested (Jumpponen 2001). The presence of Hypocreales (class Sordariomycetes) and Mortierellales (class Zygomycetes) in our dataset confirm the results of the previous meta-analysis of Bates et al. (2010). In the latter survey no arbuscular mycorrhizal (AM) fungi were found, while our study revealed the orders Archaeosporales, Diversisporales and Paraglomerales, albeit with low abundance of ca. 0.3 % of reads. In arid environments, there is evidence that nutrient transformation and exchange between BSCs and patchy plant vegetation is mediated by fungal networks of dark septate and AM fungi (Hawkes 2003, Collins et al. 2008, Green et al. 2008). Black meristematic fungi, a phylogentically diverse group of fungi, are known to be tolerant to extreme environmental conditions. For instance, they are capable to survive high doses of radiation and tolerate desiccation. One stress-resistance mechanism is the accumulation of melanin in cell walls that play an important role in tolerating excessive heat or cold, extreme pH or osmotic conditions, polychromatic UV-radiation. Beside melanin, other protective compounds are, for instance, mycosporines. They act as shields against UV radiation or protect the cell by scavenging reactive oxygen species (Gostinčar et al. 2012, Selbmann et al. 2013).

Many investigations have been carried out to determine the extent which BSCs promote or inhibit the growth of higher plants. BSCs coverage can play an important role in affecting individual plants at different stages of their life cycle, including seed germination, seedling survival and establishment, and plant growth (cf. Eldrige & Greene 1994, Prasse & Bornkamm 2000, Harper & Belnap 2001, Belnap et al. 2003, Pendleton et al. 2003, Li et al. 2005, Su et al. 2009, Godinez-Alvarez et al. 2011). The larger supply of available nutrients and water in BSCs than in open soils could be an advantage for the establishment and growth of higher plants. However, the nutrient content in BSCs is generally very low, including N, even though some cyanobacteria (e.g. *Anabaena, Nostoc, Gloeocapsa*) and cyano-lichens (e.g. *Collema*) are able to fix N from atmosphere (Wang et al. 1981, Belnap 2002, 2003, Aranibar et al. 2003, Evans & Lange 2003). This implies stress and interspecific competition for resources of all living organisms within the BSCs, in which organisms that have the lowest requirements of resources (e.g. microorganisms, lichens and bryophytes) may have advantage. Additionally, we also found the establishment of higher plants on the Hochtor/Plattenkar could be inhibited by subsequent reasons: i) the mechanical barrier formed by compact BSCs hinder the penetration and growth of seedling's roots; ii) the strong freeze- and thaw movements on the BSCs surface destroy fine roots of seedlings; iii) the temperature of moist BSCs may be lower than those of open soils. Lichens and even bryophytes may also suppress the growth of higher plants physically or by releasing inhibitory substances (Poelt 1985, Zamfir 2000). Vascular plants are often absent from the vicinity of lichen patches, suggesting some adaptive strategies of the symbiotic slow-growing organisms against their higher-biomass producing competitors (Lawrey 2009, Favero-Longo & Piervittori 2010).

The occurrence of acidophilic and calcifuge plants on the Hochtor/ Plattenkar may be due to the availability of Fe (see Tyler 1996, Lee 1999, Zohlen & Tyler 2000, Führer 2005). According to Lovley (1997) and Benz et al. (1998), humus substances are utilized as electron acceptors by various bacteria that contribute indirectly to the Fe mobilization. At the end of such redox reaction cascades, plant available Fe^{2+} ions can be produced and support the growth of acidophilic plants. These processes are confirmed in the master thesis of Reitbauer (2010) by analysing the concentration of Fe in plant tissue of "acidophilic plants" which occur on the calcareous Plattenkar. According to Weber et al. (2006), a wide phylogentic diversity of microorganism is capable of dissimilatory Fe(III) reduction. At pH values at or above 7, microbial iron redox cycling can have a noteworthy effect on the geochemistry of hydromorphic soils. In terrestrial environments, microorganisms in the family Geobacteraceae, that have been detected in our data, are among the most common Fe(III)-reducing microorganisms. In addition, members of the phylum Acidobacteria can also contribute to Fe(III) reduction.

To conclude, it can be said that BSCs influence alpine ecosystems in many ways. They have an effect on the physical and chemical properties of soils and thus influence the entire soil biocoenosis, in particular the microorganisms that own high diversity and biomass. The diversity of lichens on the Hochtor is surprisingly higher than at other sites of the SCIN project (Büdel et al. 2014). For vascular plants, the effects of BSCs are quite complex, and here more research have to be carried out. In addition, airborne dust plays a vital role in the investigated alpine ecosystem as a resource for minerals, clay, and humus particles that have an effect both on plant growth and soil morphology. Much remain still unclear in different scientific fields, but we may gain a better insight into the functioning and complex biocoenosis of alpine BSCs at the end of the SCIN project.

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References

Anderson D. C., Harper K.T. & Holmren R.C., 1982: Factors influencing development of cryptogamic soil crusts in Utah deserts. J. Range Manage. 35, 180–185.

Anderson I. C. & Cairney J. W.G., 2004: Diversity and ecology of soil fungal communities: increased understanding through the application of molecular techniques. Environ. Microbiol. 6, 769–779.

Aranibar J.N., Anderson I.C., Ringrose S. & Macko S.A., 2003: Importance of nitrogen fixation in soil crusts of southern African arid ecosystems: acetylene reduction and stable isotope studies. J. Arid Environ. 54, 345–358.

Auer I., Böhm R., Leymüller M. & Schöner W., 2002: Das Klima des Sonnblicks – Klimaatlas und Klimatopographie der GAW Station Sonnblick einschließlich der umgebenden Gebirgsregionen. Österreichische Beiträge zur Meteorologie und Geophysik 28. Zentralanstalt für Meteorologie und Geodynamik, Wien, 408 S.

Bates S.T., Garcia-Pichel F. & Nash III T.H., 2010: Fungal components of biological soil crusts: insights from culture-dependent and culture-independent studies. In: Nash III T. H. (ed.): Biology of Lichens – Symbiosis, Ecology, Environm. Monitoring, Systematics, Cyber Applications. Biblioth. Lichenol. 105, 197–210.

Belnap J., 2002: Nitrogen fixation in biological soil crusts from southeast Utah, USA. Biol. Fert. Soils 35, 128–135.

Belnap J., 2003: Factors influencing nitrogen fixation and nitrogen release in biological soil crusts. In: Belnap J. & Lange O. L. (eds): Biological soil crusts: structure, function, and management. Ecol. Stud. 150, 241–261.

Belnap J. & Gardner J. S., 1993: Soil microstructure of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. Gt. Basin Nat. 53, 40–47.

Belnap J. & Lange O. L. (eds.), 2003: Biological soil crusts: structure, function, and management. Ecol. Stud. 150, 502 S.

Belnap J., Prasse R. & Harper K.T., 2003: Influence of biological soil crusts on soil environments and vascular plants. In: Belnap J. & Lange O. L. (eds.): Biological soil crusts: structure, function, and management. Ecol. Stud. 150, 281–300.

Benz M., Brune A. & Schink B., 1998: Anaerobic and aerobic oxidation of ferrous iron at neutral pH by chemoheterotrophic nitrate-reducing bacteria. Arch. Microbiol. 169, 159–165.

Biermayer G. & Rehfuess K.E., 1985: Holozäne Terrrae fuscae aus Carbonatgesteinen in den Nördlichen Kalkalpen. Z. Pflanzenernaehr. Bodenk. 148, 405–416.

Blum W. E.H., Spiegel H. & Wenzel W.W., 1996: Bodenzustandsinventur – Konzeption, Durchführung und Bewertung. Institut für Bodenforschung, Universität für Bodenkultur. Wien, 102 S.

Blume H.P. & Schwertmann U., 1969: Genetic evaluation of profile distribution of aluminum, iron, and manganese oxides. Soil Sci. Soc. Amer. Proc. 33, 438–444.

Büdel B., 2002: Diversity and ecology of biological crusts. Prog. Bot. 63, 386–404.

Büdel B., 2003: Synopsis: Comparative biogeography of soil crust biota and communities. In: Belnap J. & Lange O.L. (eds.): Biological soil crusts: structure, function, and management. Ecol. Stud. 150, 141–152.

Büdel B., 2005: Microorganisms of biological crusts on soil surface. In: Buscot F. & Carma A. (eds.): Microorganisms in soils: roles in genesis and function. Soil Biol. 3, 307–325.

Büdel B., Colesie C., Allan Green T.G., Grube M., Lázaro Suau R., Loewen-Schneider K., Maier S., Peer T., Pintado A., Raggio, J., Ruprecht U., Sancho L., Schroeter B., Türk R., Weber B., Wedin M., Westberg M., Williams L. & Zheng L.J., 2014: Improved appreciation of the functioning and importance of biological soil crusts in Europe – the Soil Crust International project (SCIN). Biodivers Conserv. 23, 1639–1658.

Castillo-Monroy A.P., Bowker M.A., Maestre F. T., Rodríguez-Echeverría S., Martinez I., Barraza-Zepeda C.E. & Escolar C., 2011: Relationships between biological soil crusts, bacterial diversity and abundance, and ecosystem functioning: Insights from a semi-arid Mediterranean environment. J. Veg. Sci. 22, 165–174.

Collins S.L., Sinsabaugh R.L., Crenshaw C. & Green L., 2008: Pulse dynamics and microbial processes in aridland ecosystems. J. Ecol. 96, 413–420.

Concostrina-Zubiri L., Martinez I., Rabasa S.G. & Escudero A., 2014: The influence of environmental factors on biological soil crust: from a community perspective to a species level approach. J. Veg. Sci. 25, 503–513.

Cornell R.M. & Schwertmann U., 1996: The iron oxides: structure, properties, reactions, occurences, and uses. Wiley-VCH, 573 S.

Duffy L., 2011: Mikroreliefbedingte Raummuster von Böden, äolischen Substraten und Flugstäuben im Hochgebirgskarst der Nördlichen Kalkalpen (Reiteralpe, Berchtesgadener Alpen). Diss. Ludwig-Maximilian-Universität München, 131 S.

Eldridge D.J.,1993: Cryptogam cover and soil surface condition: effects on hydrology on a semiarid woodland soil. Arid Soil Res. Rehabil. 7, 203–217.

Eldridge D.J. & Greene R. S.B., 1994: Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. Aust. J. Soil Res. 32, 389–415.

Eldridge D.J. & Leys J.F., 2003: Exploring some relationships between biological soil crusts, soil aggregation and wind erosion. J. Arid Environ. 53, 457–466.

Elliott D. R., Thomas A.D., Hoon S.R. & Sen R., 2014: Niche partitioning of bacterial communities in biological crusts and soils under grasses, shrubs and trees in the Kalahari. Biodivers. Conserv. 23, 1709–1733.

Evans R.D. & Lange O.L., 2003: Biological soil crusts and ecosystem nitrogen and carbon dynamics. In: Belnap J. & Lange O.L. (eds.): Biological Soil Crusts: Structure, Function, and Management, Ecol. Stud. 150, 263–279.

Exner Ch., 1964: Erläuterungen zur Geologischen Karte der Sonnblickgruppe. Geologische Bundesanstalt, 170 S.

Favero-Longo S.F. & Piervittori R., 2010: Lichen-plant interactions. J. Plant Interac. 5, 163–177.

Fink M.H., 1984: Das Karstgebiet beim Hochtor (Hohe Tauern, Salzburg-Kärnten). Die Höhle 35 (Festschrift H. Trimmel), 127–134.

Fischer M.A., Adler W. & Oswald K., 2005: Exkursionsflora für Österreich, Liechtenstein und Südtirol. Land Oberösterreich, Biologiezentrum der OÖ Landesmuseen, Linz, 1392 S.

Foster A.J., 2011: Long-term application of poultry litter to improve soil aggregate stability under cool and warm season grasses. Turk. J. Field Crops. 16, 108–116.

Franz H., 1943: Die Landtierwelt der mittleren Hohen Tauern. Denkschr. Akad. Wiss. Wien; Math. Naturwiss. Kl. 107, 552 S.

Franz H., 1945: Untersuchungen über die Kleintierwelt ostalpiner Böden II. Die Collembolen. Zool. Jb. (Syst.) 77, 81–162.

Franz H., 1969: Besiedlung der jüngst vom Eis freigegebenen Gletschorvorfelder und ihrer Böden durch wirbellose Tiere. Neue Forschungen im Umkreis der Glocknergruppe. Wiss. Alpenvereinshefte H. 21, 291–299.

Frey W., Frahm J.P., Fischer E. & Lobin W., 1995: Die Moos- und Farnpflanzen Europas. 6. völlig neu bearb. Aufl. G. Fischer Verlag, Stuttgart, Jena, New York, 426 S.

Fritz A., 1976: Pollen im Sahara-Staub. Carinthia II 166, 173–174.

Führer C., 2005: Das Auftreten acidophiler/calcifuger Pflanzenarten in Kalk-Halbtrockenrasen. Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultäten der Georg-August-Universität zu Göttingen, 316 S.

Garcia-Pichel F., López-Cortés A. & Nübel U., 2001: Phylogenetic and morphological diversity of Cyanobacteria in soil desert crusts from the Colorado Plateau. Appl. Environ. Microbiol. 67, 1902–1910.

Garcia-Pichel F., Johnson S.L., Youngkin D. & Belnap J., 2003: Small-scale vertical distribution of bacterial biomass and diversity in biological soil crusts from arid lands in the Colorado Plateau. Microb. Ecol. 46, 312–321.

Godinez-Alvarez H., Morin C. & Rivera-Aguilar V., 2011: Germination, survival and growth of three vascular plants on biological soil crusts from a Mexican tropical desert. Plant Biol. 14, 157–162.

Gold W.G., Glew K.A. & Dickson L. G., 2001: Functional influences of cryptobiotic surface crusts in an alpine tundra basin of the Olympic Mountains, Washington, USA. Northwest Sci. 73, 315–326.

Gostinčar C., Muggia L. & Grube M., 2012: Polyextremotolerant black fungi: oligotrophism, adaptive potential, and a link to lichen symbioses. Front. Microbiol. DOI:10.3389/fmicb.2012.00390.

Green L. E., Porras-Alfaro A. & Sinsabaugh R.L., 2008: Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland. J. Ecol. 96, 1076–1085.

Grims F., 1999: Die Laubmoose Österreichs. Catalogus Flora Austriae. II. Teil, Bryophyten (Moose) Hf. 1, Musci (Laubmoose). Biosystematics and Ecology Series 15.

Gruber F., 1980: Die Verstaubung der Hochgebirgsböden im Glocknergebiet. In: Franz H. (Hrsg.): Untersuchungen an alpinen Böden in den Hohen Tauern 1974–1978, Stoffdynamik und Wasserhaushalt. Veröff. Österr. MaB-Hochgebirgsprogramms Hohe Tauern, Bd. 3. Österr. Akad. Wiss., Wagner, Innsbruck, 69–91.

Harper K.T. & Belnap J., 2001: The influence of biological soil crusts on mineral uptake by associated vascular plants. J. Arid Environ. 47, 347–357.

Hartl H. & Peer T., 2005: Nationalpark Hohe Tauern – Pflanzen. Nationalpark Hohe Tauern Wissenschaftliche Schriften, 199 S.

Hawkes C.V., 2003: Nitrogen cycling mediated by biological soil crusts and arbuscular mycorrhizal fungi. Ecology. 84, 1553–1562.

Haybach G., 1971/72: Zur Collembolenfauna der Pasterzenumrahmung im Glocknergebiet (Hohe Tauern). Verh. Zoo. Bot. Ges. Wien 110/111, 7–36.

Haybach G.,1992: Zur Collembolenfauna verschiedener Gebirgsstandorte in Österreich. Verh. Zoo. Bot. Ges. Wien 129, 159–214.

Henrikson E. & Simu B., 1971: Nitrogen fixation by lichens. Oikos 22, 119–121.

Heuberger H., 1968: Die Alpengletscher im Spät- und Postglazial. Eiszeitalter u. Gegenwart 19, 270–275.

Huber K., Peer T., Tschaikner A., Türk R. & Gruber J.P., 2007: Characteristics and function of soil crusts in different successional stages in alpine environments, outlined on an alpine lime scree in the Grossglockner region (Austria). Mitt. Österr. Bodenkundl. Ges. 74, 111–126.

Hütter C.M., 2014: Grenzwanderung über das Hochtor. In Ibetsberger H., Steyrer H., Hejl E. & Schrott L. (Hg.): Grenzwanderungen. Natur- und Kulturerlebnisführer der Universität Salzburg, Bd. 3, Universität Salzburg, Pfeil, 121–130.

Janatková K., Reháková K., Doležal J., Simek M., Chlumská Z., Dvorský M. & Kopecký M., 2013: Community structure of soil phototrophs along environmental gradients in arid Himalaya. Environ. Microbiol. 15, 2505–2516.

Janik V. & Schiller H., 1960: Charakterisierung typischer Bodenprofile der Gjaidalm. Mitt. Österr. Bodenkundl. Ges. 4, 31–44.

Jumpponen A., 2001: Dark septate endophytes – are they mycorrhizal? Mycorrhiza. 11, 207–211.

Krainer K., 2005: Nationalpark Hohe Tauern – Geologie. Nationalpark Hohe Tauern Wissenschaftliche Schriften, 199 S.

Kubiena W.L., 1948: Entwicklungslehre des Bodens. Springer, 215 S.

Kubiena W.L., 1950: Bestimmungsbuch und Systematik der Böden Europas. Enke, 392 S.

Küfmann C., 2008: Flugstaubeintrag und Bodenbildung im Karst der Nördlichen Kalkalpen. Nationalpark Berchtesgaden, Forschungsbericht 54, 159 S.

Lawrey J.D., 2009: Lichen chemical defense. In: White J. & Torre M. (eds.): Diversity of Defensive Mutualisms, 167–181.

Lee J. A., 1999: The calcicole-calcifuge problem revisited. Adv. Bot. Res. 29, 1–30.

Li X.R., Jia X.H., Long L.Q. & Zerbe S., 2005: Effects of biological soil crusts on seed bank, germination and establishment of two annual plant species in the Tengger Desert (N China). Plant Soil 277, 375–385.

Lovely D.R., 1997: Microbial Fe(III) reduction in subsurface environments. FEMS Microbiol. Rev. 20, 305–313.

Maier S., Schmidt T.S.B., Zheng L., Peer T., Wagner V. & Grube M., 2014: Analyses of dryland biological soil crusts highlight lichens as an important regulator of microbial communities. Biodivers. Conserv. 23, 1735–1755.

Meusel H., 1935: Wuchsformen und Wuchstypen der europäischen Laubmoose. Nova Acta Leopold. N. F. 3, 119–277.

Moquin S.A., Garcia J.R., Brantley S.L., Takacs-Vesbach C.D. & Shepherd U.L., 2012: Bacterial diversity of bryophyte-dominant biological soil crusts and associated mites. J. Arid. Environ. 87, 110–117.

Munsell, 1970: Revised Standard Soil Color Charts. Fujihira Industry C. Ltd., Tokyo.

Nagy M.L., Garcia-Pichel F. & Pérez A., 2005: The prokaryotic diversity of biological soil crusts in the Sonoran Desert (Organ Pipe Cactus National Monument, AZ). FEMS Microbiol. Ecol. 54, 33–245.

Nationalpark Hohe Tauern und Österreichischer Alpenverein (Hrsg.), 2000: Geo-Trail Tauernfenster. Naturkundlicher Führer, Nationalpark Hohe Tauern Bd. 19, 80 S.

Nestroy O., Aust G., Blum W.E.H., Englisch M., Hager H., Herzberger E., Kilian W., Nelhiebel B., Ortner G., Pecina E., Pehamberger A., Schneider W. & Wagner J., 2011: Systematische Gliederung der Böden Österreichs. Österreichische Bodensystematik 2000 in der revidierten Fassung von 2011. Mitt. Österr. Bodenkundl. Ges. 79, 96 S.

Nestroy O., Krupp A.Ch. & Skrowronek A., 2013: Orientierende Untersuchungen über den Einfluss von Substrat, Klima und Zeit auf die Bildung roter (Paläo-) Böden in Österreich. Mitt. Österr. Bodenkundl. Ges. 80, 65–119.

ÖNORM L 1061, 1988: Physikalische Bodenuntersuchungen. Bestimmung der Korngrößenverteilung des mineralischen Feinbodens. Österr. Normungsinstitut Wien, 1–4.

ÖNORM L 1083, 1989: Chemische Bodenuntersuchungen. Bestimmung der Acidität. Österreichisches Normungsinstitut Wien, 1–3.

ÖNORM L 1084, 1989: Chemische Bodenuntersuchungen. Bestimmung von Carbonat. Österr. Normungsinstitut Wien, 1–4.

Parker S.S., 2010: Buried treasure: soil biodiversity and conservation. Biodivers. Conserv. 19, 3743–3756.

Patzelt G., 1972: Die spätglazialen Stadien und postglaziale Schwankungen von Ostalpengletschern. Ber. Dt. Bot. Ges. 85, 47–57.

Peer T., 1993: Die Bodenformen im Sonderschutzgebiet Piffkar. Wissenschaftliche Mitteilungen aus dem Nationalpark Hohe Tauern, Bd. 1, 34–42.

Peer T., 2009: Zur Entstehung und Bedeutung von biologischen Bodenkrusten im alpinen Raum. In: Ländlicher Raum. Online-Fachzeitschrift des BMLFUW. www.laendlicher-raum.at

Peer T., Türk R., Gruber J.P. & Tschaikner A., 2010: Species composition and pedological characteristics of biological soil crusts in a high alpine ecosystem, Hohe Tauern, Austria. Eco. mont 2, 5–12.

Peer T., Türk R. & Gruber J.P., 2011: Alpine Vegetation und Böden im Karstgebiet zwischen Hochtor und Kärntner Schareck. In: Steyrer H., Hejl E., Ibetsberger H. & Schrott L. (Hg.): Hohe Tauern – Naturkundliche Exkursionen. Natur- und Kulturerlebnisführer der Universität Salzburg, Bd. 2, Universität Salzburg, Pfeil, 116–128.

Pendleton R. L., Pendleton B.K., Howard G.L. & Warren S.D., 2003: Growth and nutrient content of herbaceous seedlings associated with biological soil crusts. Arid Land Res. Manag. 17, 271–281.

Pérez F.L., 1997: Microbiotic crusts in the high equatorial Andes, and their influence on paramo soils. Catena 31, 173–198.

Poelt J., 1969: Bestimmungsschlüssel europäischer Flechten. Lehre, 757 S.

Poelt J., 1985: Über auf Moosen parasitierende Flechten. Sydowia, Annales Mycologici Ser. II, 39, 241–254.

Poelt J. & Vězda A., 1977: Bestimmungsschlüssel europäischer Flechten. Ergänzungsheft I. J. Cramer, 258 S.

Poelt J. & Vězda A., 1981: Bestimmungsschlüssel europäischer Flechten. Ergänzungsheft II. J. Cramer, 390 S.

Prasse R. & Bornkamm R., 2000: Effect of microbiotic soil surface crusts on emergence of vascular plants. Plant Ecol. 150, 65–75.

Reháková K., Chlumská Z. & Dolezal J., 2011: Soil cyanobacterial and microalgal diversity in dry mountains of Ladakh, NW Himalaya, as related to site, altitude, and vegetation. Microb. Ecol. 62, 337–346.

Reitbauer V., 2010: Zum calcicolen-calcifugen Komplex. Das Vorkommen „acidophiler" Gefäßpflanzen auf Karbonatböden im Glocknergebiet. Masterarbeit, Universität Salzburg, 105 S.

Sattler B., Remias D., Lütz C., Dastych H. & Psenner R., 2010: Leben auf Schnee und Eis. In: Koch E.-M. & Erschbamer B. (Hg.): Glaziale und periglaziale Lebensräume im Raum Obergurgel. Alpine Forschungsstelle Obergurgl 1, Innsbruck, 229–251.

Schüller H., 1969: Die CAL-Methode, eine neue Methode zur Bestimmung des pflanzenverfügbaren Phosphates in Böden. Z. Pflanzenernähr., Düng. Bodenkde. 123, 48–63.

Schwertmann U., 1964: Differenzierung der Eisenoxide des Bodens durch Extraktion mit Ammoniumoxalat-Lösung. Z. Pflanzenern. Düng. Bodenk. 105, 194–202.

Schwertmann U. & Taylor R.M., 1977: Iron oxides. In: Dixon J. B., & Weed S. B. (eds.): Minerals in soil environments: Soil Sci. Soc. America, 145–180.

Seckbach J. & Oren A., 2010: Microbial Mats: Modern and Ancient Microorganisms in Stratified Systems. Cellular Origin, Life in Extreme Habitats and Astrobiology, Vol 14. Springer, Dordrecht.

Selbmann L. , Grube M., Onofri S., Isola D. & Zucconi L., 2013: Antarctic epilithic lichens as niches for black meristematic fungi. Biology 2, 784–797.

Sellstedt A. & Richau K.H., 2013: Aspects of nitrogen-fixing Actinobacteria, in particular free-living and symbiotic Frankia. FEMS Microbiol. Lett. 342, 179–86.

Steven B., Gallegos-Graves L.V., Belnap J. & Kuske C.R., 2013: Dryland soil microbial communities display spatial biogeographic patterns associated with soil depth and soil parent material. FEMS Microbiol. Ecol. 86, 101–113.

Sticher H., Bach R., Brugger H. & Vökt U., 1975: Flugstaub in vier Böden aus Kalk, Dolomit und Serpentin (Schweizer Jura und Schweizer Alpen). Catena 2, 11–12.

Su Y.G., Li X.R., Zheng J.G. & Huang G., 2009: The effect of biological soil crusts of different successional stages and conditions on the germination of seeds of three desert plants. J. Arid Environ. 73, 931–936.

Türk R. & Gärtner G., 2003: Biological soil crusts of the subalpine, alpine, and nival areas in the Alps. In Belnap J. & Lange O. L. (eds.): Biological soil crusts: structure, function, and management. Ecol. Stud. 150, 67–73.

Türk R. & Hafellner J., 2010: Nachtrag zur Bibliographie der Flechten in Österreich. – Biosystematics & Ecology Series No 27, Verlag der Österreichischen Akademie der Wissenschaften, 1–381.

Tyler G., 1996: Mineral nutrient limitations of calcifuge plants in phosphate sufficient limestone soil. Ann. Bot. 77, 649–656.

Veit H., 1993: Holocene solifluction in the Austrian and southern Tyrolean Alps: dating and climatic implications. Paläoklimaforschung 11, 23–32.

Visconti F., de Paz J.M. & Rubio J.L., 2010: What information does the electrical conductivity of soil water extracts of 1 to 5 ratio (w/v) provide for soil salinity assessment of agricultural irrigated lands? Geoderma 154, 387–397.

Wang F., Zhung Z. & Hu Z., 1981: Nitrogen fixation by an edible terrestrial blue-green alga. In Gibson A.H., Newton W.E. (eds.): Current Perspectives in Nitrogen Fixation. Elsevier, Amsterdam, 455 S.

Weber K.A., Achenbach L.A. & Coates J.D., 2006: Microorganisms pumping iron: anaerobic microbial iron oxidation and reduction. Nature Rev. Microbiol. 4, 752–764.

West N.E., 1990: Structure and function of soil microphytic crusts in wildland ecosystems of arid and semiarid regions. Adv. Ecol. Res. 20, 179–223.

Wilke B.M., 2005: Determination of chemical and physical soil properties. In: Margesin R. & Schinner F. (eds): Manual of Soil Analysis – Monitoring and Accessing Soil Bioremediation. Springer, 47–95.

Williams K.P., Sobral B. W. & Dickerman A.W., 2007: A robust species for the Alphaproteobacteria. J. Bacteriol. 189, 4578–4586.

Wirth V., Hauck M. & Schultz M., 2013: Die Flechten Deutschlands. Eugen Ulmer, 1244 S.

WRB, World reference base for soil resources, 2006: A framework for international classification, correlation and communication. World soil resources reports. Food and agriculture organization of the United Nations (FAO), Rome. ftp://ftp.fao.org/agl/agll/docs/wsrr103e.pdf

Yeager C.M., Kornosky J.L., Housman D.C., Grote E.E., Belnap J. & Kuske C.R., 2004: Diazotrophic Community Structure and Function in Two Successional Stages of Biological Soil Crusts from the Colorado Plateau and Chihuahuan Desert. Appl. Environm. Microbiol. 70, 973–983.

Zamfir M., 2000: Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. Oikos 88, 603–611.

Zhang B., Zhang Y., Downing A. & Niu Y., 2011: Distribution and composition of cyanobacteria and microalgae associated with biological soil crusts in the Gurbantunggut desert, China. Arid Land Res. Manag. 25, 275–293.

Zohlen A. & Tyler G., 2000: Immobilization of tissue iron on calcareous soil –differences between calcicole and calcifuge plants. Oikos 89, 95–106.

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