

The role of
microorganisms and
plants in ecosystem
development

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The role of microorganisms and plants at different stages of ecosystem development for soil formation

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Abstract

Soil formation is the result of a complex network of biological as well as chemical and physical processes. Mainly the role of soil microbes is of high interest in this respect, as they are responsible for most transformations and drive the development of stable and labile carbon and nutrient pools in soil, which facilitate the basis for the subsequent establishment of plant communities. Glacier forefields, which provide a chronosequence of soils of different age due to the continuous retreat of the ice layer as a consequence of the increasing annual temperature since the last centuries, are a nice play ground to study the interaction of bacteria, fungi and archaea with their abiotic environment at different stages of soil formation. In this review we give insights into the role of microbes for soil development on the basis of investigations which have been performed at the Damma glacier in Switzerland in the frame of two international network projects Big Link (<http://www.cces.ethz.ch/projects/clench/BigLink>) and DFG SFB/TRR 38 (<http://www.tu-cottbus.de/ecosystem>). The review focusses on the microbiology of three major steps of soil formation including weathering of the parental material, the development of basic nutrient cycles, the formation of soil crusts and biofilms as initial microbial network structures and the occurrence of plants respectively the setup of plant communities.

1 Introduction

Microbial communities can be considered as architects of soils (Rajendhran and Gunasekaran, 2008) and many ecosystem services that are linked to terrestrial ecosystems, including plant production, safeguarding of drinking water or carbon sequestration are closely linked to microbial activities and their functional traits (Torsvik and Ovreas, 2002). Vice versa the soil matrix as well as chemical and physical properties of soils like quality and amount of soil organic matter, pH, redox conditions, have a pronounced influence on the dynamics of microbial community structure and function in

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soils (Lombard et al., 2011). This close interplay between abiotic conditions and the soil biosphere is one of the most fascinating issues in earth sciences with huge implications for environmental as well as human health (van Elsas et al., 2008). Taking these complex interactions networks between biota and their abiotic environment into account, not surprisingly soil development is a long term process and the formation of soils with high fertility levels may be a result of more than 1000 yr of soil “evolution” (Harrison and Strahm, 2008). Therefore, mainly in times of global change and the subsequent threats for soils, mainly the loss of soil quality, there is a huge need to improve our understanding how this interplay in soil develops and to identify factors that drive the formation of soils, to develop strategies for a sustainable protection of soils for future generations (Doran, 2002).

To study the development of interactions between abiotic and biotic soil properties is a highly complex issue, taking into account the different spatial and temporal scales that might influence the development of biotic networks in soils (Ollivier et al., 2011). Microbes act on a scale of μm^3 and form biogeochemical interfaces with the soil matrix, shaping their own environment on (Totsche et al., 2010). How these interfaces are connected and how many different interfaces are needed for the stability of soils and resilience development on larger scales for fields is not known so far. Furthermore, microbes can change their phenotype in between minutes depending on the environmental conditions present at those interfaces by gene induction or repression (Sharma et al., 2012). The corresponding transcripts have often half times in the range of seconds to minutes. Putting this in the frame of soil formation which may take centuries is a highly challenging issue.

In addition the diversity of soil microbes is huge and can be considered still as a black box (Simon and Daniel, 2011); consequently so far nobody is able to give exact numbers on the species or even more important ecotype richness in one unit of soil. Microbes are also able to easily exchange genetic information, which induces a very fast and ongoing diversification of organisms in natural environments and the genetic flexibility of the whole soil microbiome can be considered as enormous (Monier et al.,

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2011). Finally, most functional traits, for example the degradation of plant litter or the development of food web structures and closed nutrient cycles, are a result not of a single organism but of microbial communities which closely interact with each other (Aneja et al., 2006). Even the development of symbiotic interactions between plants and microbes in soil (e.g. mycorrhization of plants or legume – rhizobia interactions) are much more complex than described in text books, including the involvement of a diverse number of “helper organisms” during the infection phase (Frey-Klett et al., 2007). Time scales for community development and stable microbiomes are therefore still a highly challenging topic of research and in many cases not even concepts exist for the formation of microbial communities on the basis of single organisms being present at a certain time point of ecosystem genesis.

In recent years the forefields of receding glaciers has been recognized as an ideal field site to study the initial steps of soil formation and to get insights into the formation of organismic interactions as well as the formation of abiotic – biotic soil interfaces, as in a close area of some square kilometres a chronosequence of soils of different age classes and development stages can be found and compared. Since the end of the Little Ice Age around 150 yr ago, most alpine glaciers have been receding at an increasing rate (Frank et al., 2004). A recent survey on 97 Swiss glaciers revealed that today most glaciers show an annual recession of dozens of meters (Frank et al., 2007). A similar trend can be observed in alpine zones dominated by permafrost. The level of permanent permafrost is steadily decreasing (Frank et al., 2007). Detailed studies on glacier recession and soil formation have been performed at the Damma Glacier in Central Switzerland (Kobierska et al., 2011). The length of this glacier has been monitored since 1921 and the rate of recession is currently about 10 m per year (<http://glaciology.ethz.ch/swiss-glaciers/>). The forefield has a northeastern exposition, an inclination of about 21 % and is located at 2050 m a.s.l. (<http://map.geo.admin.ch/>). As a result of two brief advancements of the glacier two little moraines (dated 1928 and 1992) can be observed in the forefield.

In this review we would like to summarize our current knowledge, which could be generated from respective studies at the Damma glacier in Switzerland in the last decades and show how we were able to improve our current picture on soils as the most important bioreactor on earth based on current data from glacier forefield chronosequence approaches (Fig. 1).

2 Setting stage for microbial activity: the role of weathering

The formation of fertile soils from inorganic bedrock implies a complex interaction of physical, chemical and biological processes. The rate of the soil development is dominated by variables such as climate, bedrock type, topography, time, microorganisms and plants (Paul and Clark, 1996). Usually hundreds of years are required to convert inorganic precursors to humus and eventually distinct soil horizons.

The climate in alpine zones is characterized by high precipitation and pronounced fluctuations of temperatures. For example, in the cities of Basel, Bern and Zurich (Switzerland, all at an altitude of < 550 m a.s.l.) the annual precipitation is in the range of 140–160 cm yr⁻¹ (<http://www.meteosuisse.admin.ch/web/en.html>). In contrast, in the Alps, at an altitude of > 2500 m a.s.l., the precipitation is usually > 250 cm. Nevertheless, in parts of the glacier forefield which are dominated by rocks and sand with a low water holding capacity microorganisms can be subject to dry stress. In addition, solar radiation (UV and visible range) increases with altitude due to decreasing optical air masses (Blumenthaler et al., 1997). For UVB, the increase is about 9% per 1000 m and in high altitude glacier forefields, severe effects of UVB on microorganisms cannot be excluded. UVB damage results from a direct absorption of radiation by target molecules such as DNA and proteins and usually microorganisms produce secondary metabolites as a photo protective mechanism.

However, in the mountains not only the radiation at daytime but also the back radiation at night time is higher than in the lowlands. As a consequence, the temperature fluctuations on the rock and soil surfaces are very pronounced and can easily go

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fluorescence staining of biofilms on mineral surfaces or scanning electron microscopy of weathered minerals) and do not necessarily allow a predicting of the rates of biological weathering under field conditions. Direct field observations are rare and include for example a study on the role of microorganisms in phosphate cycling in the Damma glacier forefield (Tamburini et al., 2010).

For the establishment of microbial life in a glacier forefield both the chemical composition of the bedrock as well as the physical structure of the weathered fractions are important. Siliceous rocks contain a number of minerals which contain essential elements (e.g. apatite is a source of phosphorous) and thus favour microbial life. In contrast, the weathering of calcareous rocks releases very few elements which facilitate the growth of microorganisms. Some rocks such as serpentinites even release toxic elements (e.g. Nickel, cadmium) which prevent plant life (Bratteler, 2006) and which may also inhibit microbial activities.

Soil aggregation is of utmost importance in controlling microbial structures and functions and plant life. Ideally, the weathered fractions in a glacier forefield include sand (fraction 2 mm to 63 μm), silt (63 to 2 μm) and clay (< 2 μm) and thus allow a good diffusion of gases and bacterial motility as well as high ion exchange and water holding capacities. Particularly clay is often found in glacier forefields (Kobierska et al., 2011) and it is essential for aggregate formation and the stabilization of soil organic matter (Paul and Clark, 1996).

In the Damma glacier forefield, there is little change in the phyllosilicate clay mineralogy, whereas the amount of poorly crystalline Fe oxides and Al phases increased with soil development, reflecting a growing potential for SOC stabilization (Dümig et al., 2011). In contrast to strongly increasing quantities, only small changes in the composition of the Fe and Al pools were detected during initial pedogenesis. Fe oxides and inorganic Al phases mainly remained poorly crystalline.

3 Development of initial C and N cycles

In abiotic initial soils, geochemical processes are dominated by chemical reactions, such as mineral dissolution or hydrolysis. Chemical reactions are enhanced by physical weathering that increases the soil surface and so the number of reactive surfaces.

At the same time, an increased surface area favors the colonization by microorganisms, which will catalyze and accelerate the geochemical cycles. At the Damma glacier important macronutrients, such as phosphorus (P) and sulfur (S) are part of the mineral composition. Therefore, microbial activity might accelerate the release of those elements from the bedrock to supply living organisms with P and S. In contrast, carbon (C) and nitrogen (N) are not part of the mineral composition and are scarce in the initial soils, stressing the importance of studying these geochemical cycles from the view of microorganisms.

In the initial soils total *carbon* (C) content ranges from 700–1100 $\mu\text{g C g}^{-1}$ (Brankatschk et al., 2011; Bernasconi et al., 2011). Microbial C is comparatively high (10–50 $\mu\text{g C g}^{-1}$, Brankatschk et al., 2011; Bernasconi et al., 2011), indicating a high turnover rate of C. This is in agreement with soil respiration rates, which are in the range of 130 $\mu\text{g C g}^{-1} \text{ a}^{-1}$ (calculated from Gülland et al., 2013). The source of organic carbon in the initial soils however is a matter of controversy. Three different sources potentially contribute C to the initial soil. First, deposition of allochthonous organic matter, such as plant litter, insects, and soot particles contribute considerable amounts of C (Hodkinson et al., 2003). Measurements of allochthonous C deposition range from 7.5 $\text{kg C ha}^{-1} \text{ a}^{-1}$ at the Damma glacier (Brankatschk et al., 2011) to 34 $\text{kg C ha}^{-1} \text{ a}^{-1}$ at Toolik Lake, Alaska (Fahnestock et al., 1998). Second, C inputs from close-by cyanobacterial and algal communities, such as cryoconite holes or patches of snow algae, might contribute C to the forefield (Sawstrom et al., 2002). Third, ancient carbon might be present in the Damma glacier forefield. During the Holocene, glacier basins were vegetated. Dating the sub-fossil remains of trees and peat, warm periods, e.g. around the years 2000, 3900 and 4900 BP were identified (Joerin et al.,

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the only protective mechanism as poorly crystalline Fe phases also interact with OM by co-precipitation or microaggregation. These results show that organo-mineral associations already evolve in early stages of soil development, whereby mineral weathering and OM accumulation proceed in different timescales (Dümig et al., 2012).

5 Different pools of *nitrogen* (N) are present in the initial soils. Content of total N ranges from 70 to 100 $\mu\text{g N g}^{-1}$ (Brankatschk et al., 2011; Bernasconi et al., 2011), while the contents of microbial N ($6 \mu\text{g N g}^{-1}$), nitrate ($0.13 \mu\text{g N g}^{-1}$), and ammonium ($0.03 \mu\text{g N g}^{-1}$) are considerably lower (Brankatschk et al., 2011). As for C, different N sources contribute N to the glacier forefield: (i) N fixation by microorganisms and (ii) N
10 deposition. N fixation is very low in the initial soils at Damma glacier. Duc et al. (2009), detected N fixation activity of in the range of $2 \text{ pmol C}_2\text{H}_4 \text{ g}^{-1} \text{ h}^{-1}$, using the acetylene reduction assay. Another study found that N fixation below $0.2 \text{ pmol N h}^{-1} \text{ g}^{-1}$ in the initial soils, using the stable isotope incorporation method (Brankatschk et al., 2011). The low N fixation activity was accompanied by low abundance of the N fixation
15 marker gene *nifH* (2×10^6 copies g^{-1}) confirming the presence of few microorganisms capable of the N fixation process. In contrast to N fixation, the deposition of N is orders of magnitude higher. Estimations for wet deposition of nitrate and ammonium range between 7 and 11 $\text{kg N ha}^{-1} \text{ a}^{-1}$. Total N deposition is estimated to be
20 10 to 15 $\text{kg N ha}^{-1} \text{ a}^{-1}$. This indicates the importance of N deposition as primary N source in the forefield and is supported by stable isotope measurements. The N in the initial soils exhibits $\delta^{15}\text{N}$ values of -4 to -2 , which appear to be typical for initial soils in cold climate and can be explained by the negative $\delta^{15}\text{N}$ of atmospheric N (Smittenberg et al., 2012). Quantification of organic detritus on snow revealed that approximately $0.6 \text{ kg N ha}^{-1} \text{ a}^{-1}$ is deposited as particulate organic matter. Decomposition and mineralization of this organic matter was suggested to be the dominant
25 N transformation process in the initial soils at the Damma glacier (Brankatschk et al., 2011). Similarly, Bardgett and Walker (2004) described a heterotrophic stage of C decomposition at Ödenwinkelkees glacier, Austria. Respiration measurements support this notion, as microbial activity and breakdown of organic matter is comparatively

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high in the initial soils. During three summer months 33 g C m^{-2} were respired cumulatively while C pool size was 90 g C m^{-2} (Gülland et al., 2013). Also, the marker genes for the breakdown of organic matter, chitinase (*chiA*) and protease (*aprA*), were detected in the initial soils. Abundance of *chiA* gene was 7×10^5 copies g^{-1} and *aprA* gene was quantified with 6×10^6 copies g^{-1} . Activities of other N turnover processes such as nitrification and denitrification were low ($< 2 \text{ nmol N g}^{-1} \text{ h}^{-1}$) in the initial soils (Brankatschk et al., 2011). Nevertheless, the abundance of the marker gene for nitrification *amoA* of ammonium oxidizing bacteria (AOB) was comparatively high in the initial soils (2×10^6 copies g^{-1}). Abundance of ammonium oxidizing archaea *amoA*, in comparison, was 3×10^4 copies g^{-1} (Brankatschk et al., 2011). In the initial soils might be ideal conditions for AOB because ammonium is supplied from atmospheric deposition and mineralization of organic matter. At the same time, competition for ammonium, e.g. by plants, is low. Therefore, the high abundance of AOB seem reasonable. However, potential nitrification measurements were low and did not support that hypothesis (Brankatschk et al., 2011). From the analyzed marker genes for denitrification, the *nirK* gene was the most abundant one with 1.5×10^8 copies g^{-1} . Since potential denitrification activity was low, the high *nirK* gene abundance might indicate the presence of facultatively anaerobic bacteria in the initial soils, and would support the hypothesis of the dominance of mineralizing microorganisms that are adapted to temporarily waterlogged conditions, e.g. during heavy rains, snow melt. Figure 2 provides an idea on the development of the microbial nitrogen cycle during soil formation. The established C and N cycle in the glacier forefield leads to the accumulation of protein-rich organic matter in the very early stages of soil development, which with time includes a stronger accumulation of carbohydrate-rich material, both most probably of microbial origin (Dümig et al., 2012).

Phosphorous and *sulfur* are present in the minerals of the bedrock and can derive from deposition.

Phosphorus (P), next to N, is frequently found to be the limiting nutrient in terrestrial ecosystems. Therefore, the release of P from the minerals in the bedrock was at the

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center of studies at the Damma glacier. The granite bedrock contains approximately 400–600 $\mu\text{g P g}^{-1}$ soil that is bound to apatite and the amount of organic P in the initial soil is low (50–60 $\mu\text{g P g}^{-1}$) (Tamburini et al., 2010; Göransson et al., 2010). An even smaller proportion of the P, however, is freely available as phosphate (0.8 $\mu\text{g P g}^{-1}$) as determined by resin bag experiments (Bernasconi et al., 2011). Nevertheless, the heterotrophic microorganisms in the initial soils were found not to be limited by P. The leucine incorporation method was used to test which of the major nutrients C, N or P limits microbial growth (Göransson et al., 2011). It was shown that C is the limiting nutrient for microorganisms in the initial soil. Similarly, the plants were not limited by the P availability. The C/P ratio of the plants indicated sufficient P is available throughout the forefield, even in the initial soils, which had low phosphate concentrations (Göransson et al., 2011). Albeit P deposition is expected to be in the range of 0.1–1.2 $\text{kg P ha}^{-1} \text{a}^{-1}$ (BAFU, Phosphorflüsse der Schweiz, 2009), the P from the bedrock is the most important P source in the glacier forefield. Isotopic analysis of the plants P source showed that the minerals are the major P source and deposition plays a minor role (Tamburini et al., 2010). This might underline the microbial importance of mineral dissolution during the initial soil formation process. The dissolution of P and other nutrients from the minerals might be accelerated by microorganisms releasing organic acids or chelators. This was investigated in mineral dissolution experiments using bacterial isolates from the Damma forefield (Lapanje et al., 2012). Selected isolates were screened for high mineral dissolution potential; however, the abiotic controls using citric and hydrochloric acid released elements at significantly higher rates than did the bacterial isolates (Lapanje et al., 2012). Future studies need to investigate the P release from mineral bedrock in the initial soils, as the mechanisms have not been studied in detail, but are crucial for the development of the ecosystem.

Significant amounts of sulfur (S) are required to maintain the high ecosystem productivity that was measured at the Damma forefield (Smittenberg et al., 2012). In the bedrock a total of approximately 5 $\mu\text{g S g}^{-1}$ is present (Lazzaro et al., 2009; Bernasconi et al., 2011) and concentrations of available sulfate in the initial soils range from

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0.15–0.30 $\mu\text{g S g}^{-1}$ (Noll and Wellinger, 2008). However, in the developed soils the S content is in the range of 300 $\mu\text{g S g}^{-1}$ (Bernasconi et al., 2011). Borin et al. (2010) pointed out the importance of sulfuroxidising bacteria as first colonisers in microbial communities at the Midtre Lovénbreen glacier, Svalbard. If similar processes prevail at the Damma glacier this would indicate that sulfate is quickly released from the minerals of the initial soil and might therefore be plant available early on. A study on desulfonating bacteria, i.e. bacteria that release sulfate from organic matter, found very high diversity at the Damma forefield (Schmalenberger and Noll, 2010). Therefore, it was hypothesised S might be a limiting nutrient. As indicated above, S content in the soil is low in the initial soils and S stocks in the developed soil cannot be explained by mineral dissolution only. Therefore S deposition might significantly contribute to the S budget of the forefield. The deposition of S is estimated to be 200 to 350 $\text{mg SO}_x \text{m}^{-2} \text{a}^{-1}$ (Nyiri et al., 2009), however detailed analysis on S sources in the Damma forefield, e.g. deposition measurements or isotope analysis, are lacking.

4 Biofilms and soil crusts as hotspot of nutrient turnover

Initial sites of glacier forefields are characterized by less vegetation and low nutrient contents. In 2005 the vegetation cover at the Damma glacier was below 20 % at a distance of 80 m to the glacier front, which corresponds to approximately 13 yr of soil development (Hämmerli et al., 2007). Therefore, it is obvious that initial processes of soil formation and input of nutrients rely on the activity of microorganisms. In principal two main functions can be assigned to the microbes: (i) biological weathering of the bedrock material and (ii) formation of interfaces for nutrient turnover at vegetation free sites.

Regarding biological weathering, Frey et al. (2010) demonstrated that isolates from the granitic sand in front of the Damma glacier were able to effectively dissolve the siliceous bedrock material. The main underlying mechanism for the dissolution is the formation of biofilms on the mineral surface. Organisms being organized in such

biofilms exude organic acids like oxalic acid, which on the one hand lead to a ligand-promoted dissolution and on the other to a proton-promoted dissolution because of the decreasing pH. The released elements are then captured in the polysaccharide matrix of the biofilm and display therefore a nutrient hotspot in the bare substrate.

5 Anyhow, it was assigned by several researchers that the trophic base at initial sites of glacier forefields is established by first colonizers like *Cyanobacteria*, green algae, lichens, mosses and fungi, which often conglomerate and form biological soil crusts (BSC) (Belnap et al., 2001a). The formation of BSC is strongly linked to the environmental conditions present, as well as to the parental material. Figure 3 shows the
10 development of BSCs in a laboratory study on different parental materials obtained from selected initial sites. These BSC fulfill different important roles in ecosystem development. Most BSC forming organisms are able to perform photosynthesis and/or nitrogen fixation and thus enhance carbon and nitrogen content of the soils. In this regard, researchers stated that the performance per unit ground surface under optimal conditions of BSC is similar or even higher than that of vascular plants (Yoshitake
15 et al., 2009; Pointing and Belnap, 2012). Moreover, Dickson et al. (2000) showed that the N_2 -fixation activity of BSC was already measurable at 3 °C. Thus, the “vegetation period” of BSC starts much earlier than that of vascular plants and nutrient input is prolonged, which is especially advantageous at glacier forefields. Nutrient acquisition
20 is further supported by the excretion of exopolysaccharides by several *Cyanobacteria*, which are often coated with clay particles. The negatively charged clay particles are in turn associated with positively charged nutrients and prevent those for leaching (Belnap et al., 2001a). At the Damma glacier highest numbers of *Cyanobacteria* have been found at the initial sites including *Lecanoromycetes*, where a lot of lichen-forming species belong to (Zumsteg et al., 2012). A second study, which focused on
25 *nifH*-carrying microbes, revealed a cyanobacterial community comparable to mature BSC from the Colorado plateau (Duc et al., 2009; Yeager et al., 2004). The dominant species were *Nostoc* sp. and *Scytonema* sp. Both are able to produce pigments, which enable them to withstand high solar radiation. This property is a big advantage

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at glacier forefields because radiation strongly increased during summer times and day temperatures can reach up to 40 °C at the soil surface (Miniaci et al., 2007), while the thermal radiation at night hampered the storage of heat energy from the day (Landolt, 1992). Thus, poikilohydric organisms, which form BSC, have a big advantage as they are able to withstand drought and high solar radiation and as soon as they are rewetted activity strongly increased. Although, crust forming organisms have been detected at initial sites of the Damma glacier, crust formation at the sampling site was not observed (Duc et al., 2009). This observation is in contrast to findings of Bernasconi et al. (2011), who detected mosses as well as lichens at initial sites. Anyhow, this might be mainly attributed to the exposed position of some parts of the initial sites to the glacier tongue, which leads to regular disturbances of the surface by the glacial stream. However, as soon as sites are more protected against erosion, because of the moraines or they are located in hydrologic islands, moss dominated crusts develop, which is in accordance with observations in the Negev desert (Israel) (Zaady et al., 2000). Interestingly, these crusts are often associated with vegetation patches (Duc et al., 2009). However, it is very likely that crusts have been there before plants established, as they are known to pave the way for vascular plants, because on the one hand BSC improve soil fertility and on the other hand they create advantageous micro-environments for plant germination and growth (Belnap et al., 2001b).

Regarding soil fertility, data from different BSC indicated that crusted soils comprise 200 % higher nitrogen contents than uncrusted soils (Harper and Belnap, 2001; Rogers and Burns, 1994; Pointing and Belnap, 2012). Interestingly, Johnson et al. (2007) revealed that the nitrogen input via N₂-fixation is similar to the nitrogen export by leaching or exudation. Thus, BSC itself stay nitrogen limited while the surrounding soil accumulates nitrogen. Brankatschk et al. (2011) demonstrated that deposited nitrogen and carbon are important driver for ecosystem development at initial sites, the ability of *Cyanobacteria* to trap nutrient-rich deposits via their exopolysaccharide sheath even facilitates that effect (Reynolds et al., 2001). Thus, also decomposing microbes are stimulated in BSC, which in turn supply plants in the vicinity with a lot of different

micro-nutrients and trace elements. As arctic and alpine plant species often comprise a shallow root system, because of the thin soil layers, they can easily acquire the nutrient sources below the BSC (Billings, 1987).

BSC did not only enhance soil nutrient status but also improve physical conditions for plant establishment. The rough surface structure and dark color of BSCs create beneficial conditions for seedling settlement and germination, because they are sheltered against external disturbances and temperature is higher compared to bare surrounding soils (Escudero et al., 2007; Breen and Lévesque, 2008; Gold, 1998). Moreover, the stress for pioneering plants is generally reduced. On the one hand because of the already mentioned nutrient conditions and on the other hand the volumetric water content is higher in BSC (Breen and Lévesque, 2008). Altogether, BSCs are able to buffer the diurnal changes in climatic conditions at glacier forefields and therefore reduce stress conditions, which otherwise might hamper plant development.

Although, a lot of effort is still necessary to directly characterize the BSC at the Damma glacier forefield, a lot of data indirectly underline their pivotal role in ecosystem development. In summary, one can assign several functions to BSC and biofilms at the Damma glacier forefield. At the beginning of soil formation microorganisms organized in biofilms contribute to the weathering of bedrock material and the dissolution of trace elements. Afterwards, their main function is the input of nutrients to the bare soil and the stabilization of the surface. This is than the basis for the settlement and growth of plants, which will finally completely replace BSC.

5 Role of plants

During the succession at the Damma glacier forefield coverage of plants increased with soil age from 20 % to 70 % (Hämmerli et al., 2007). Plants play an important role in the stabilization of the slope (Körner, 2004) and soil development, as their root exudates and decaying litter material are the main sources of organic matter at initial sites of the glacier forefield (Duc et al., 2009). Although, microbial biomass is much lower at

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initial sites the decomposition of plant material is as fast as at developed sites over a time period of twelve weeks (Esperschütz et al., 2011). Interestingly, initial sites of the Damma glacier and other Alpine glaciers are dominated by forbes and grasses like *Leucanthemopsis alpina*, *Agrostis gigantea* or *Cerastium uniflorum* whereas legumes like *Lotus alpinus* or *Trifolium pallescens* appear later in succession, although their symbiosis with rhizobia might be an advantage at nitrogen poor initial sites (Miniaci et al., 2007; Göransson et al., 2011; Tschërko et al., 2003). There are two reasons explaining the absence of legumes from the initial sites: First, many legumes like *Lotus alpinus* form heavier seeds than *L. alpina* or *C. uniflorum* (Pluess et al., 2005; Tackenberg and Stöcklin, 2008) and thus the dispersal via wind is more difficult. Second, the establishment and maintenance of a rhizobia-legume symbiosis is a very energy consuming process (Merbach et al., 1999) and therefore energy consumption might be too high under these harsh conditions. However, in contrast to Alpine glacier forefields, at Glacier Bay (Alaska) symbiotic N-fixers like *Dryas drummondii* or single species of alder are already dominant at initial sites. That difference might be mainly attributed to climatic conditions. While at Glacier Bay a mild and maritime climate with small annual and diurnal temperature changes predominates, the Damma glacier forefield is characterized by strong temperature variations and irregularly distributed rainfall during the year, both being unfavorable for effective plant establishment (Bernasconi, 2008; Landolt, 1992; Miniaci et al., 2007).

Anyhow, several studies at the Damma glacier showed that pioneering plants display a nutrient hotspot at initial sites (Töwe et al., 2010; Duc et al., 2009; Miniaci et al., 2007). Thus, much higher abundances and activities of microbes were detected in the rhizosphere of pioneering plants. In initial soils this effect is even expanded up to a distance of 20 cm (Miniaci et al., 2007). The phenomenon of enhanced microbial activity and abundance in the rhizosphere of plants is known as the “rhizosphere effect” (Butler et al., 2003; Hartmann et al., 2008). Regarding the Damma glacier the rhizosphere effect is generally more pronounced at initial sites compared to developed ones (Töwe et al., 2010; Edwards et al., 2006). This observation seems to be a general effect

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independent from plant species, bedrock material or climatic conditions. For example, Deiglmayr et al. (2006) detected only a significant difference in the nitrate reductase activity at the initial sites of the Rotmoosferner glacier. This activity was 23 times higher in the rhizosphere of *Poa alpina* compared to the bulk soil. The enhancement of microbial activity and abundance in the rhizosphere is mainly attributed to uncontrolled leakage or controlled exudation of organic substances like malate, citrate or oxalate. Thus, it is unquestionable that plants display a nutrient hotspot in terms of carbon as they provide up to 40 % of the photosynthetically fixed CO₂ to the microbes (Paterson and Sim, 2000). In return, microbes supply the plant with nitrogen, phosphate or other nutrients and additionally protect them against herbivores or parasites.

Interestingly, highest abundances of nitrogen fixers in the bulk soil in connection with highest nitrogen fixation activity in the rhizosphere of *L. alpina* have been detected at intermediate development stages, where nitrogen content is still low but plant coverage had already strongly increased, which hints at a competition between microbes and plants for nitrogen (Brankatschk et al., 2011; Duc et al., 2009). This theory is further corroborated by results from Töwe et al. (2010) where the abundance of *nifH* carrying microbes was highest in the rhizosphere of *L. alpina* planted in a 10-yr soil, which was connected with lowest C/N ratios of the plant biomass (Fig. 4). However, during incubation the nitrogen content of *L. alpina* grown in the 10-yr soil strongly increased, which fits with the assumption that microbes are able to win the competition over a short timescale, because of their higher volume-surface ratio, higher growth rate and substrate affinity (Hodge et al., 2000). On the contrary, plants are more effective over a long time period, because of their longer lifespan and the ability to retain the assimilated nitrogen (Hodge et al., 2000; Nordin et al., 2004). In addition to the enrichment of nitrogen fixing microbes also heterotrophic mineralisers like *chiA*-containing microbes are enhanced (Tscherko et al., 2004; Töwe et al., 2010). The degradation of chitin or proteins has the advantage that low weight organic compounds consisting of carbon and nitrogen are released. The ability of plants to assimilate amino acids, amino sugar or small peptides seems to be ubiquitously distributed among different

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ecosystems and plays a particular role in cold and wet habitats (Näsholm et al., 2009; Lipson and Monson, 1998; Schimel and Bennett, 2004). In parallel functional groups leading to nitrogen losses like nitrifying or denitrifying microbes were reduced in the rhizosphere, which is in line with the assumption that plants are able to actively influence their rhizosphere community (Singh et al., 2004) by changing their exudation pattern or by actively excreting substances like tannins, polyphenolic substances or monoterpenes (Briones et al., 2003; Kowalchuk and Stephen, 2001; Ward et al., 1997; Cocking, 2003). In this regard, Edwards et al. (2006) detected changes in the exudation pattern of *L. alpina* along the Damma glacier forefield mainly attributed to a strong reduction of oxalic and citric acid concentrations. In general it seems that indeed microbial activity and abundance is much higher in the rhizosphere of pioneering plants compared to the bulk soil, but the community composition is strongly driven by the bulk soil community, whereas at developed sites the plant selects for special microbes (Duc et al., 2009; Miniaci et al., 2007). The strength of that phenomenon has been proven for functional groups like *nifH*-containing microbes as well as for overall bacterial diversity from different sites and by different methods like PLFA analysis (Tscherko et al., 2004; Bardgett and Walker, 2004), clone libraries (Duc et al., 2009), pyrosequencing (Knelman et al., 2012) and finger printing methods (Deiglmayr et al., 2006; Miniaci et al., 2007).

With ongoing succession a shift from a competition for nitrogen to a competition for phosphate takes place (Vitousek and Farrington, 1997). While phosphate is not limited at the beginning of succession as it is released during weathering of the siliceous bedrock material, the concentration of bioavailable phosphate is steadily decreasing along the glacier chronosequence and thus favouring ecto- and ericoid mycorrhizal associations (Bernasconi et al., 2011). A similar trend was found at Glacier Bay (Alaska), where symbiosis with legumes have been found already at very young soils but first mycorrhiza-forming plants appear later in succession (Chapin et al., 1994).

Anyhow, as soon as vegetation cover is nearly closed ecosystem development speeds up so that ecosystem properties are similar to mature ecosystems. Beside others this includes increasing amounts of organic carbon and nitrogen, the formation of

soil horizons, increasing microbial biomass and enzyme activities even in the bulk soil (Dümig et al., 2011; Brankatschk et al., 2011; Duc et al., 2009; Sigler and Zeyer, 2002). Once a stable plant community has developed, a positive feedback loop establishes. The plant still provides fixed CO₂ via rhizodeposition to the microbial community. Additionally, the high input of dead plant material provides a broad nutrient source for decomposing microbes. Thus, in contrast to sparsely vegetated sites, sufficient amounts of nitrogen are released during mineralization of high molecular compounds, which is then again available for plants. Moreover, climatic conditions like water content, temperature or radiation are more stable below a closed plant cover, leading to a reduction of environmental stressors, which are strongly pronounced in initial poorly vegetated sites.

Finally, one can summarize that plants play a crucial role in ecosystem development, but their function changed during succession. At initial stages their pivotal role in stabilizing the slope and providing carbon is unquestionable, but similarly they compete for scarce nutrients like nitrogen with the microbes. The succession of plant establishment strongly depends on the external conditions. Thus, at alpine glacier forefields higher plants establish later compared to glacier forefields with maritime climate where shrubs and small trees can be already found at very young sites (Bardgett and Walker, 2004).

6 Outlook

Overall the data provided so far clearly shows major factors driving the formation of soils at sites with retreating glaciers. Although it can be assumed that in other initial ecosystems overall the same factors might be of importance for soil development, the relevance of each single factor might change, thus a direct transfer of the obtained results, e.g. for developing strategies for the restoration of sites after, e.g. open pit mining activities, may not be possible. However, the phases described in this review, including weathering of the parental material, the development of basic nutrient cycles,

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the formation of soil crusts and biofilms as initial microbial network structures and the occurrence of single plants respectively the setup of plant communities, can be also found during the development of other ecosystems. As the data provided from glacier chronosequence studies has shown the outstanding roles of plants for soil development, future research strategies for the generation of management strategies for site restoration thus might take this in consideration and develop strategies for active planting of selected plant species which can tolerate the harsh conditions present at initial sites.

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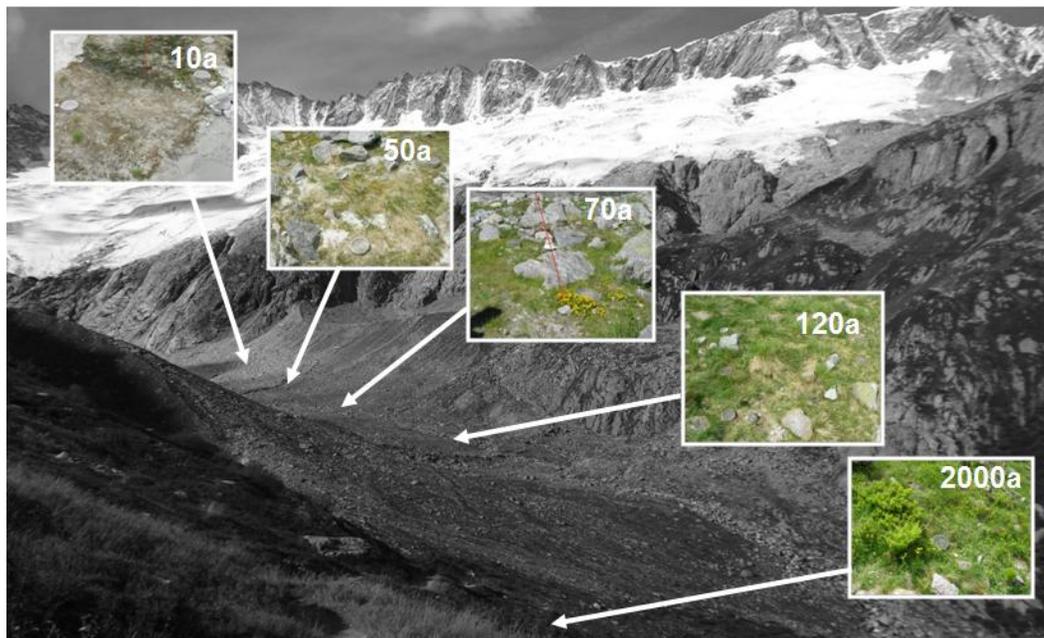


Fig. 1. The chronsequence of soils of different degree of development at the Damma glacier (Switzerland) in response to the continous retreat of the glacier.

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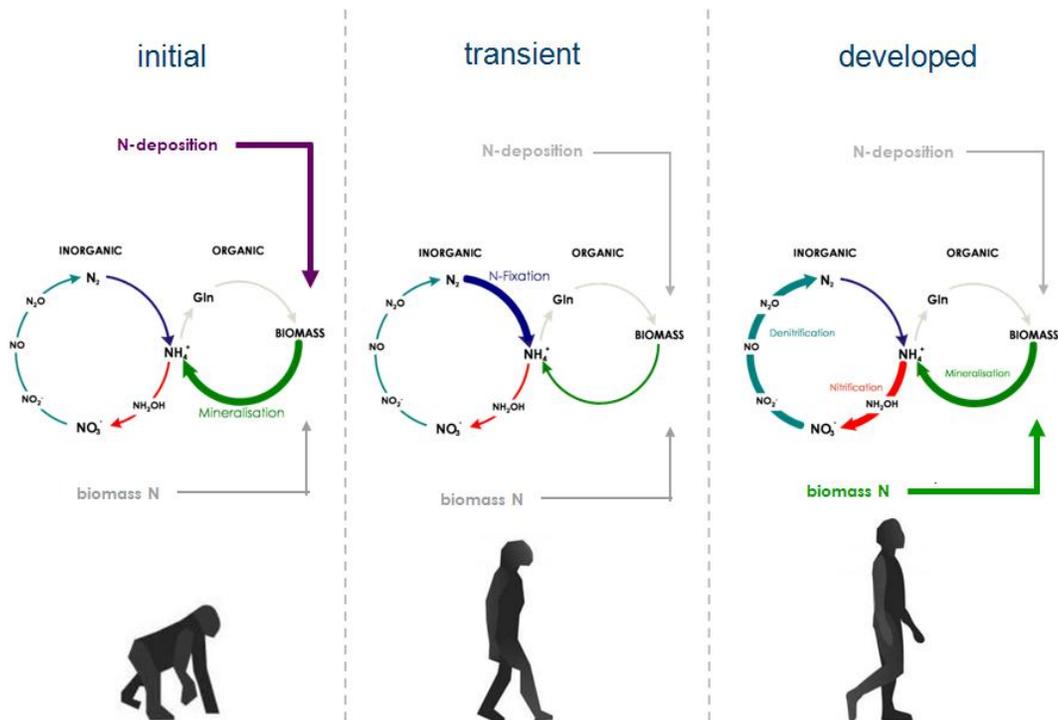


Fig. 2. The development of the microbial nitrogen cycle during soil formation.

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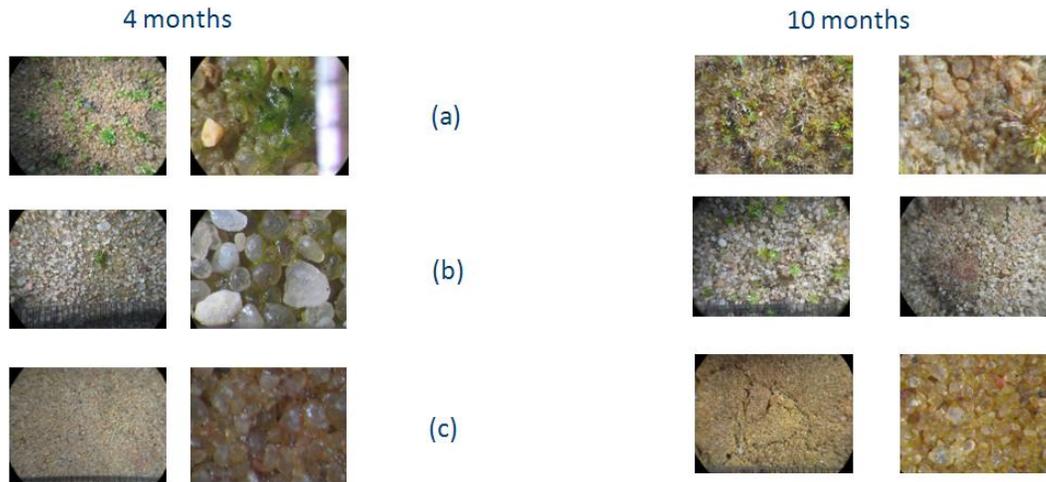


Fig. 3. The development of soil crusts in response to the parental material in a green house experiment after four and ten month of incubation. Parental material was obtained from the Chicken Creek catchment **(a)** (Gerwin et al., 2010), the Lieberose sand dunes **(b)** (Brankatschk et al., 2012) and the Abensberg sand dunes **(c)** (Voelkel et al., 2011).

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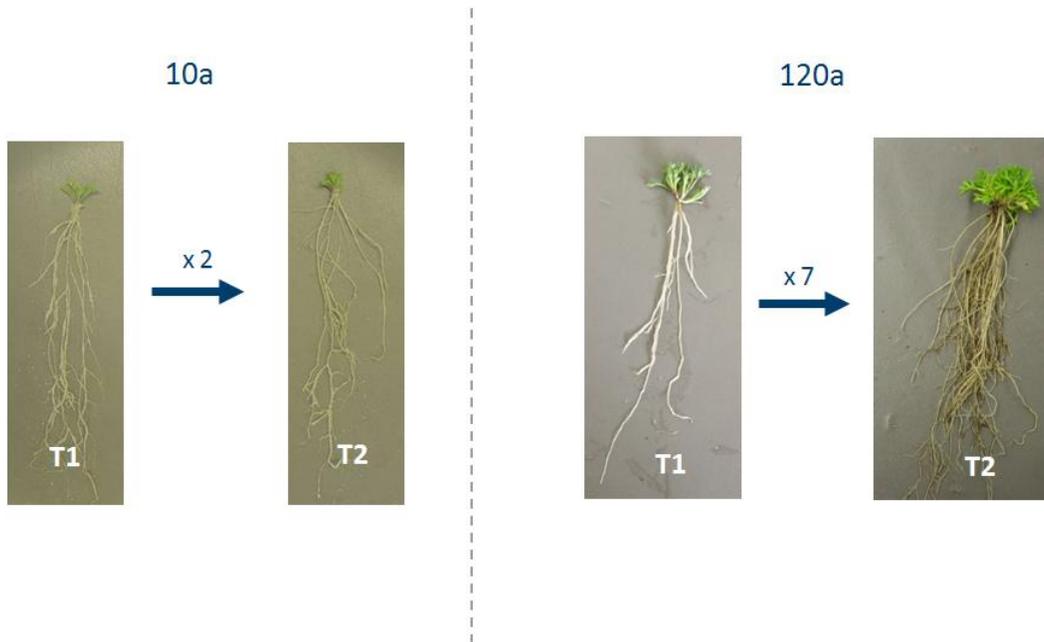


Fig. 4. Development of root biomass of *L. alpina* grown in soils obtained from the Damma chronosequence which have been ice free for 10 respectively 120 yr at two different time points of plant development (2 weeks and 8 weeks of growth) in a green house experiment.

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