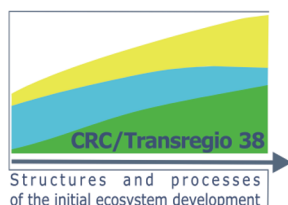


R.F. Hüttl, I. Kögel-Knabner,  
R. Schulin & W. Gerwin (eds.)

### Structures and processes of the initial ecosystem development phase in an artificial water catchment (*Final report CRC/TR 38*)





**Ecosystem Development**

**Vol. 4**

**Structures and processes of the initial ecosystem  
development phase in an artificial water catchment  
(Final report CRC/TR 38)**

Edited by

Reinhard F. Hüttl, Ingrid Kögel-Knabner,  
Rainer Schulin & Werner Gerwin



Brandenburg University of Technology Cottbus 2013

# Ecosystem Development

## Vol. 4

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## Introduction

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### 1 Objectives of CRC/TR 38

Objective of the CRC/TR 38 was the study of structures and processes of the initial ecosystem development. The importance of the starting phase of ecosystem development was discussed by the collaborative research center within two fundamental review papers. Schaaf et al. (2011) provide a general overview of relevant processes and patterns of initial ecosystems compared to mature systems. Open questions and research deficits are highlighted in this article. A second paper by Raab et al. (2012) summarizes the most important aspects of initial ecosystem processes as key factors of landscape development. In conclusion of both fundamental papers it was assumed that the initial phase is characterized by less structured and therefore less heterogeneous ecosystems. Thus, analysis of young ecosystems in their initial stages should provide better insights into ecosystem functioning.

Following this basic concept, the idea of the CRC/TR 38 was to analyze the establishment of new structures and processes which lead to a growing structuring and in consequence to a growing complexity and heterogeneity in a well-defined system. Further, with the help of this step-by-step development of the ecosystem it was aimed to learn from occurring feedbacks, which appear between old and newly emerging structures and patterns in order to better understand also the behavior of more mature systems. Special emphasis was placed on the spatial and temporal dynamics of both evolving structures and related processes and their interactions. The main hypothesis of the collaborative research center was “Initial patterns define and shape the development and later stages of an ecosystem”. Based on this the project investigated the following central hypotheses:

- (1) Initial processes of the ecosystem development are shaped by pre-existing structures.
- (2) The initial spatial structures govern water distribution, moisture conditions as well as water fluxes and transport processes within the system.
- (3) The abiotic conditions of the structured system together with establishing biota determine the formation of biological patterns. In consequence, feedback processes determine patterns of soil and humus development including element cycles.
- (4) Thresholds can be defined indicating the beginning of qualitatively and quantitatively new phases of development.

- (5) These defined phases of development of an ecosystem are reflected in the water and element budgets at the catchment scale.

Structures in this regard are e.g. biocrusts, vegetation patches or geomorphic surface patterns, soil compartments as well as hydrological structures such as flow paths or the groundwater body. Processes in general are fluxes and transformations e.g. water and matter fluxes, biological consumption or accumulation and chemical reactions. The characteristics of these structures and processes can be interpreted as indicators of the state of the whole system. In the beginning, abiotic, i.e. physical and particularly hydrological structures control the first phase of development of an ecosystem. Chemical processes become more important when the development of the system proceeds. Indeed, biotic factors appear certainly in the beginning but gain larger influence later during the development accompanied by organic matter accumulation which influences in turn the further development. Therefore, it was hypothesized as a simplified model of ecosystem development that three stages can roughly be distinguished: (1) a more or less abiotic Geo-System; (2) followed by a Hydro-Geo-System; and (3) the Bio-Hydro-Geo-System.

The studies of the CRC/TR 38 took place at a number of different investigation sites in Germany and Switzerland. An artificially created watershed called “Chicken Creek” (“Hühnerwasser”) served as the joint investigation site and enabled the consortium to study the complex interactions and feedbacks between the developing patterns and related processes at the surface of the site as well as below ground under defined boundary conditions. The catchment represents an ecosystem in the initial phase of development. Details of the site as well as results of the ongoing comprehensive ecological monitoring have been reported in the first three volumes of the scientific series “Ecosystem Development” (online available at [www.tu-cottbus.de/ecosystem/](http://www.tu-cottbus.de/ecosystem/)). An additional experimental area was available for projects of the CRC/TR 38 in the vicinity of the Chicken Creek catchment within the post-mining landscape of the open cast mine Welzow-Süd. This site covers an area of 5 ha and exhibits site conditions which are generally comparable with the artificial catchment. A set of further sites for reference purposes was investigated by the collaborative research center. These reference sites were defined as sites in the initial development phase but under different environmental conditions. Particularly, the Damma Glacier forefield in the Swiss Alps (Kanton Uri, municipality of Göschenen) (Bernasconi et al., 2011) was proved to be very well suited for these studies as a series of development stages could be investigated within a very small distance. The youngest sites are ice free for about 10 years; the oldest sites are in an age of about 2,000 years. Further, inland dunes with ages from some decades, centuries to thousands of years are further examples of reference sites under investigation, most of them in the State of Brandenburg, e.g. at a former military site near Cottbus called “Lieberose” (Brankatschk et al., 2013). Similar to the artificial catchment Chicken Creek the “Neuer



Lugteich” was established as an artificial watershed by Vattenfall Europe Mining AG in the post-mining landscape of the open-cast mine Welzow-Süd (Spröte et al., 2010).

The central objectives of the CRC/TR 38 were to

- (1) reveal which abiotic and biotic structures and processes control the initial phase of ecosystem development,
- (2) elucidate which interactions exist between processes and both abiotic and biotic patterns in the initial phase,
- (3) investigate differences between processes and patterns of initial systems compared with mature ecosystems,
- (4) derive and define different stages during ecosystem development, and to
- (5) detect parameters that allow the transfer of results to other ecosystems in an initial stage.

## **2 Central findings**

The investigations during the first funding period of the CRC/TR 38 revealed that the basic assumption of low heterogeneity and structuring of ecosystem in their initial stage was essentially correct. Further, it could be confirmed that the artificial catchment is a suitable site for this studying the development of a young ecosystem. Compared to the surrounding reclamation sites of the post-mining landscape and certainly also compared to naturally developed sites outside the mining area, the catchment appeared to be comparatively homogenous, at least immediately after the construction was finished. In general, the catchment was constructed as a landscape element with a very simple geological configuration. However, the importance of some slight differences in the composition of the dumped sandy material e.g. for the occurrence of vegetation patterns became obvious soon. In addition, internal structures due to the dumping process are still prevailing in the underground of the catchment and have great influence on the behavior of the system. The significance of such initial structures for the further evolution of the ecosystem as assumed in the central hypothesis is clearly visible.

The dynamics of the ecosystem development were in some parts unexpectedly high, and the complexity of patterns and structures increased rapidly during the first five years (Gerwin et al., 2011). With regard to the preliminary results after the first years of ecosystem development at least the first statement of the main hypothesis of the CRC/TR 38 (“initial patterns define and shape the development”) turns out to be correct. It can be stated that numerous structures evolved along identified initial patterns. In some cases the relationship

between initial and new structures is obvious. Thus, the direction of many erosion gullies is oriented along surface structures caused by large machines during the final construction steps.

Further, groundwater fluxes crossing the subsurface clay dams are producing clear patterns of increased soil moisture in specific parts of the catchment. Other dependencies are less significant and obvious and need further investigations. E.g., the development of specific vegetation patterns cannot be explained easily for some parts of the site. Also, characteristics of the groundwater behavior and related water fluxes are still not completely understood. The interesting question is how long these influences of initially formed patterns and structures will last, when the system's development is proceeding. The long-term influence of initial structures has to be analyzed, therefore, in future projects dealing with the Chicken Creek catchment.

In hypotheses 1 and 2 it was postulated that initial processes of the ecosystem development differentiate along existing structures because the initial spatial structure governs water distribution, moisture conditions as well as water fluxes and transport processes within the system. A crucial tool to validate these central hypotheses is the structure and process model provided by scientific project C5. During the first funding period the general design of this model was developed and it can be used to visualize the initial system with its main characteristics such as the topography of the surface and subsurface clay liner boundaries, substrate properties, internal structures like dumping cones etc. (cf., report of project C5; Maurer et al., 2011). It is planned to further develop this model in a new project after the ending of the CRC/TR 38. It is assumed that the model will be useful to validate the influence of abiotic conditions on the emerging biotic structures and patterns and their feedbacks as suggested in hypothesis 3.

Hypotheses 4 and 5 state that the initial ecosystem development is not regarded as a continuous, linear process but can be divided into different stages separated by thresholds. In the above mentioned model of the initial development three general states were proclaimed to be of importance: The Geo-, Hydro-Geo-, and Bio-Hydro-Geo-System phases. With regard to this it can be said that particularly the hydrological behavior of the catchment indicates that the system is still far from a (dynamic) equilibrium. Groundwater tables indeed show typical seasonal fluctuations due to evaporation losses in summer and groundwater recharge in winter, but significant influences of the growing vegetation cover on these groundwater fluctuations could not be found so far. Generally, it is obvious that the Chicken Creek system is still in a very early state. However, against the background of the very rapid development it is expected that the Bio-Hydro-Geo-System phase will be reached earlier than originally anticipated.

Additional secondary developmental stages are conceivable that do not have necessarily impact on the whole catchment scale. Despite the short observation time so far, some preliminary results indicate that already a sequence of different secondary development phases valid for compartments of the system has taken place. Considerable changes of the

vegetation cover with regard to dominant plant species were identified based on intensive vegetation surveys, carried out by project Z1 (Zaplata et al., 2013).

Numbers of plant species and individuals increased rapidly. In addition, a certain spatial differentiation of species occurrence (vegetation patches) took place. Moreover, changes of the surface forming processes could be observed. Erosion and sedimentation processes which were of extreme importance for the system development during the first two years are much reduced. This is expressed by fast growing vegetation particularly within former erosion gullies and a significant reduction of sediment input into the pond. Fig. 1 illustrates the importance of selected process groups of the observed ecosystem development based on results of the first funding period.

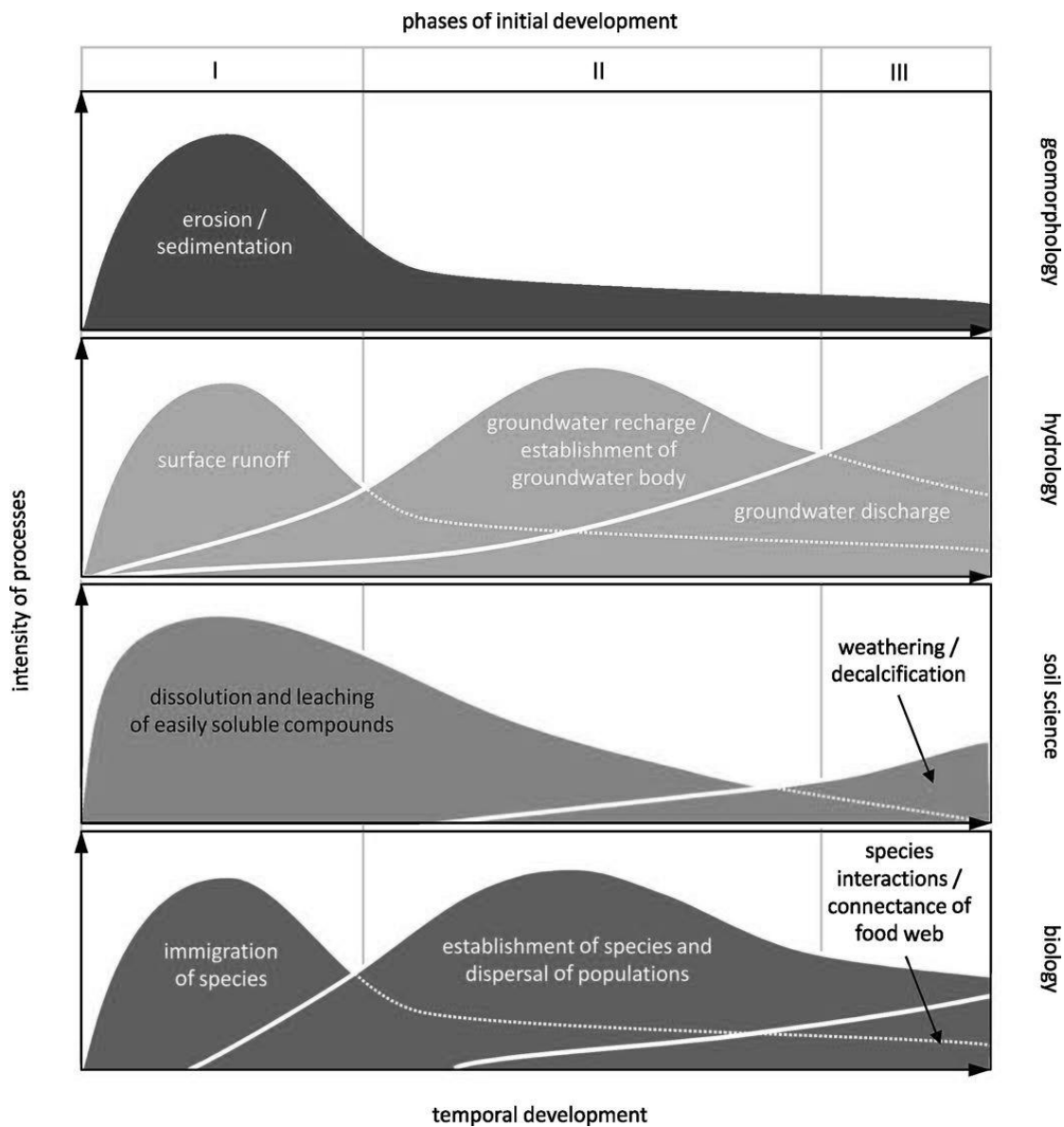


Fig. 1: Schematic overview of intensity (from low to dominating with regard to the qualitative and/or quantitative importance of the respective process at a specific moment) of selected geomorphic, hydrologic, pedogenic and biologic processes and their temporal development during the initial ecosystem stage observed at the Chicken Creek catchment (figure from: Elmer et al., 2013).

### **3 Central conclusions – relevant structures and processes**

In summary, the CRC/TR 38 was able to identify a number of structures and processes that are considered to be relevant and specific for such young systems. These results are based on the artificial catchment, and on additional results from different scientific projects as well as on findings made at reference sites, mainly in the Damma Glacier forefield. These results can be grouped as follows: (1) initial structures and heterogeneity, (2) flow paths both at the surface and in the underground, (3) soil crusts, (4) ancient organic carbon, and (5) weathering/mineralization and nutrient availability.

#### **3.1 Initial structures and heterogeneity**

Small heterogeneities caused by initial structures were of great importance for the later development of the system. E.g. slight differences of substrate properties on the artificial catchment resulted in differences of the shape of erosion gullies. Whereas the gullies in the sandy eastern part are wide, the gullies of the loamier western part are narrow and deeply incised with steep lateral slopes. It can be assumed that the diversity of the substrate has further implications on the patterns of the vegetation cover as well as on flow paths of the water in the system. Groundwater flow is probably impeded by initial structures such as dumping cones in the subsurface and Hofer et al. (2011) demonstrated the role of small-scaled heterogeneity on subsurface flow path development. In the first funding period various attempts were made to assess the heterogeneity of the system. Soil samples from the aquifer were taken immediately after the construction was finished down to the clay layer in order to document this very initial situation. These samples were taken along a regular grid that was established in the beginning of the monitoring project. In 2008 the projects A2, A3, B1 and B3 carried out a second soil sampling campaign. This campaign was designed to investigate the scale-dependent spatial variability of topmost soil material (0-3 cm) (Papritz et al., 2011). The sampling was repeated in August 2011 to look for changes in heterogeneity due to the development of new structures and patterns of the ecosystem. Results are expected in the near future. Inner structures resulting from construction processes are further examples for initial structures at the artificial catchment. Based on aerial photographs from 2004/05 these dumping structures could be integrated into the structure and process model of project C5 (Maurer et al., 2011).

#### **3.2 Flow paths**

In the very beginning of the first phase of development flow paths for water were defined widely by initial structures of the system, but most of these initial structures were formed accidentally. Therefore, important flow paths for water, e.g. for infiltration along soil macropores, still had to be established and up to now fluxes are still low.

The hydraulic conductivity of the substrate is obviously lower than expected for sandy material and discharge depends on hydrological connectivity in the subsurface as investigated by Hofer et al. (2011). Infiltration of water from precipitation is usually oriented along preferential flow paths, which are often the result of biological activities such as root growth or burrowing by insects or soil fauna (Badorreck et al., 2012). In contrast to the gradual development of preferential flow paths crusting structures were formed very rapidly on the surface of the soil. In the case of the artificial catchment both, the missing preferential flow paths and these soil crusts (see below), resulted in an unexpectedly high surface runoff which was underestimated by hydrological models (cf., project C2; Holländer et al., 2009). A dense network of rills and gullies was eroded by the surface runoff and formed corridors for small episodic streams at the backslope and permanent streams at the footslope of the catchment. The evolution of this erosion rill network could be explained accurately by modeling (Hofer et al., 2012). The naturally formed stream network controls erosion, transport and sedimentation processes which in turn have great influence on e.g. the groundwater level and the colonization patterns of vegetation.

### **3.3 Soil crusts**

Soil crusts can be of great importance in initial ecosystems. At first, physical crusting due to rain splash appeared very soon after the construction of the site was completed and led to the already mentioned unexpectedly high surface runoff. The model workshops carried out by project C2 revealed that the phenomenon of soil crusting is usually not considered by hydrological models. As a consequence, surface runoff was underestimated by the applied models. Physical crusts were described by project A4, and A3 studied the colonization of the crusts by microorganisms and their effects on hydrology (Fischer et al., 2010). These biological soil crusts are of great importance with regard to the initial stabilization of the soil surface. They potentially promote surface runoff due to sealing the surface and impeding water infiltration. Soil crusts interact with higher plant species as a crusted soil surface may prevent germination of seeds. During the first years of observation different stages of crust development were observed (Spröte et al., 2010).

### **3.4 Ancient organic carbon**

Both investigations at the Damma Glacier forefield as well as observations at the artificial watershed revealed the importance of old organic carbon for initial ecosystems. Rather unexpectedly high amounts of DOC were found at both sites. Dating the DOC confirmed the origin from ancient organic matter. Recent organic matter has still to be accumulated and the Damma chronosequence gave an estimate of the time needed for significant humus accumulation to occur (Dümig et al., 2011).

Initially available stocks of organic carbon are of great importance for microbial turnover and for the establishment of food webs in the very first stages of the development. The occurrence and meaning of old organic carbon was the objective of an ad-hoc working group that was formed by projects A2, A3, B3 and B5 during the first funding period. Results of these investigations have been published by Risse-Buhl et al. (2013).

### **3.5 Mineralization and nutrient availability**

Even if Töwe et al. (2010) could demonstrate the important role of nitrogen fixation for plants in young soils, the results of Brankatschk et al. (2011) at the Damma glacier forefield suggest that the initial nitrogen budget is dominated by decomposition of deposited organic compounds. However, on the Chicken Creek catchment leguminous herbaceous plants like *Trifolium arvense* or *Lotus corniculatus* or woody plants like *Robinia pseudoacacia* which are able to fix nitrogen from the air were frequently found. With regard to a probably heterogeneous distribution of nutrients project B1 investigated influences on the growth of plant roots (Boldt et al., 2012). Nutrient limitation and distribution might be a key for understanding the development of vegetation patterns. Nutrient mineralization from initially rare organic matter is important for young ecosystems. Esperschütz et al. (2011) investigated the decomposition of litter in young soils and found significant differences between the microbial communities of initial sites compared to well-developed soil ecosystems, particularly with regard to fungal biomass. C-transformation in the developing streams of the initial ecosystem was studied by project B5 in erosion rills of the Chicken Creek catchment as well as in artificial flumes (e.g. Gerull et al., 2012).

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## **Project A2 – Interactions between soil solution and mineral surfaces: significance for initial element cycling**

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### **1 Introduction**

Soil solution composition is an important factor controlling transport, cycling and fluxes of carbon and nutrients in ecosystems. It is linked both to mineral weathering (Lindroos et al., 2003; Raulund-Rasmussen et al., 1998) and biotic processes within ecosystems (Kelly et al. 1998; Smits et al. 2005; van Breemen et al. 2000). Soil solution dynamically interacts with the soil solid phase that can act both as source and sink for carbon and nutrients. The relevance of soil solution composition for soil formation is mainly based on chronosequence studies or on delimitation from developed soils (Lichter, 1998; Melkerud et al., 2003). Little is known about dynamic changes during initial phases of soil formation.

Mineral reactive surfaces play an important role for the accumulation and stabilization of organic matter (Eusterhues et al., 2005; Guggenberger & Kaiser, 2003; Hagedorn et al., 2003; Kaiser & Guggenberger, 2003; Kögel-Knabner et al., 2008; Kothawala et al., 2009; Qualls et al., 2004). Transport of dissolved organic carbon (DOC) is often channeled along preferential flow paths (Hagedorn et al., 2000; Hagedorn & Bundt, 2002). Neff & Asner (2001) concluded that, although microbial processes are important for DOC production and consumption, physicochemical processes such as the interaction with mineral surfaces are dominating DOC leaching (cf., Brooks et al., 1999; McDowell, 2003). More and more recent studies show that old or fossil organic carbon is a significant source for microbial processes but also for the DOC export from initial ecosystems (Bardgett et al., 2007; Hood et al., 2009; Raymond & Bauer, 2001).

Interaction between dissolved inorganic and organic constituents and mineral phases were mostly studied at the lab scale using artificial or purified minerals (Kaiser & Zech, 2000) or in situ in well developed, mostly acidic soils (e.g. Jansen et al., 2003; Lindroos et al., 2003). Conen et al. (2007) reported increasing surface areas and SOM accumulation along two chronosequences after glacier retreat, but a clear distinct influence of the mineral composition in the parent material. In chronosequences on rapidly weathering volcanic soils, Lilienfein et al. (2004) showed that sorptivity of organic nutrients and carbon initially increased with soil development. In later stages sorptivity decreased again due to an occupation of sorption sites by organic matter.

This indicates dynamic changes in the interactions between soil solid and solute phase (Fig. 1). Mineral weathering affects these interactions by generating reactive surfaces that can act as sources and sinks for dissolved elements (e.g., Deutschmann & Ludwig, 2000). With progressing soil development and accumulation of SOM these reactive surfaces are more and more saturated (Kaiser & Zech, 1998). Caner et al. (2010) showed that mineral weathering and clay formation can be observed within rather short time periods also in sandy substrates. Since soil solution composition and leaching of elements affects weathering and the formation of new mineral surfaces, there is a feedback between soil solution and weathering.

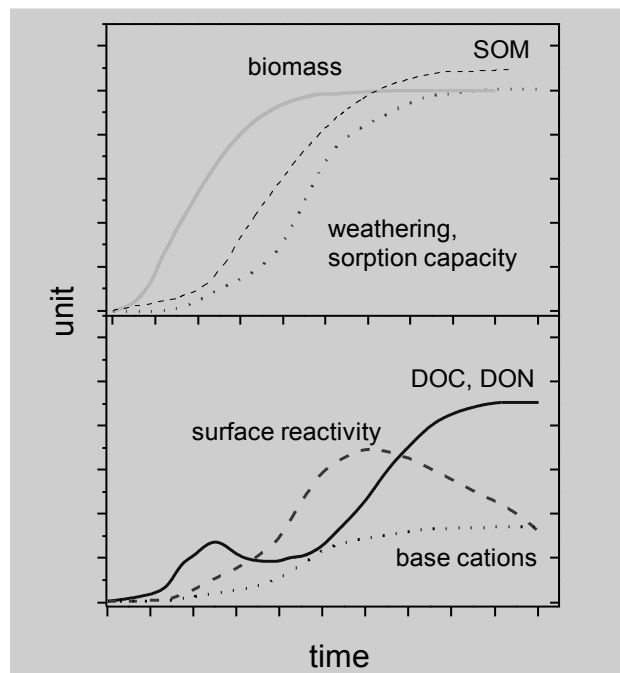


Fig. 1: Conceptual model of dynamic interactions between soil solution and soil solid phase during initial soil formation.

The source function of weathering for nutrients changes dynamically. With ongoing soil development the release of nutrients by mineral weathering gets less important compared to recycling of nutrients from decomposition of SOM. Sorption of DOM to mineral surfaces may contribute in the long-term also to nitrogen accumulation in ecosystems (Vitousek et al., 1998). Results by Neff et al. (2000) indicate that ecosystem age has an influence on DON formation and composition.

The spatial structures and patterns (e.g. erosion, vegetation) may have important effects on these interactions by affecting water fluxes through the soil, above- and belowground input of organic litter, translocation and textural sorting of mineral surfaces or microbial activity and thereby affecting soil formation rate and soil function (e.g., Haugland, 2004).

During the first phase of the CRC/Transregio 38 we mainly concentrated on

1. microcosm experiments with  $^{13}\text{C}$  and  $^{15}\text{N}$  labeled litter;
2. C flux measurements at the Damma sites;
3. tracer studies with  $^{13}\text{C}$  and  $^{15}\text{N}$  labeled litter at the Damma site;
4. geostatistical sampling within the catchment to characterize surface soil properties (collaborative initiative of subprojects A2, A3, B1, B3 and C5);
5. soil respiration measurements at Chicken Creek;
6. soil microbial activity at Chicken Creek;
7. DOC flux measurements in soil columns at the experimental field site (collaboration with subproject B3).

## 2 Results

### 2.1 Microcosm experiments

Main objectives of the microcosm experiment were to determine the transformation processes of C and N from litter decomposition within the gaseous, liquid and solid phase, the interaction with mineral surfaces and its role for the establishment of biogeochemical cycles. The microcosm experiments were established in a climate chamber at constant 10°C. In total, 48 soil columns (diameter: 14.4 cm; height: 30 cm) were filled with two different quaternary substrates (sand and loamy sand) representing the textural variation within the catchment at a bulk density of 1.4-1.5 g cm<sup>-3</sup>. The columns were automatically irrigated with artificial rainwater four times a day with 6.6 ml each (corresponding to 600 mm yr<sup>-1</sup>). The gaseous phase in the headspace of the microcosms was analyzed continuously for CO<sub>2</sub> and N<sub>2</sub>O concentrations. C and N transformation processes were studied using  $^{13}\text{C}$  and  $^{15}\text{N}$  labelled litter of two different plant species occurring at the catchment (*Lotus corniculatus*, *Calamagrostis epigejos*) that was incorporated into the microcosm surface. Litter was provided by subproject B3. All treatments including a control ran with eight replicates over a period of 40 weeks. Two additional microcosms acted as pure litter controls where substrate was replaced by glass pearls. Litter and substrate were analyzed before and after the experiment. Percolate was continuously collected and analyzed in two weeks intervals for C and N contents (including  $\delta^{13}\text{C}$ ), pH and ion concentrations (Zimmermann et al., 2009).

The initial phase is characterized by intensive leaching both from litter and substrates. Litter addition increased calcium leaching from carbonate weathering. Highest Ca<sup>2+</sup> concentrations were measured within the first 65 days of the experiment for the pure sand *L. corniculatus* treatment with maximum levels up to 137 mg Ca<sup>2+</sup> L<sup>-1</sup> (Fig. 2a).

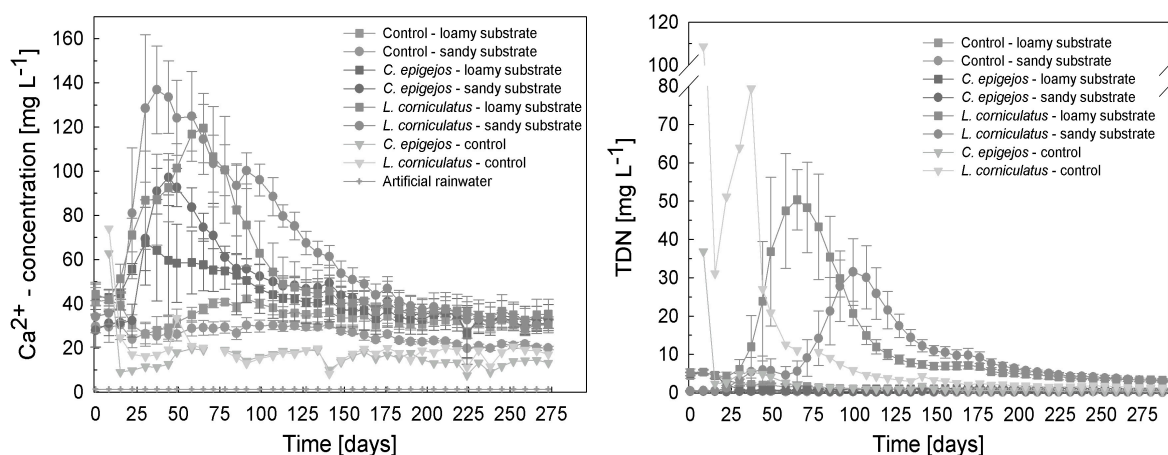


Fig. 2: Concentrations of (a) Ca and (b) TDN in the percolate of the microcosm columns with different litter treatments.

Total Ca leaching rates were highest for all *L. corniculatus* treatments resulting in Ca loss of up to 4.7 % for the loamy substrate. Litter-derived potassium released by mineralization was strongly retained in the soils by cation exchange. Only in the treatment with sandy substrate and *L. corniculatus* litter, high amounts of litter-derived potassium are leached from the columns. Initial  $K^+$  leaching from both litter controls was very high during the first weeks ( $540 \text{ mg L}^{-1}$  max. for *L. corniculatus* control) and decreased to relatively constant levels of 4-5  $\text{mg K}^+ \text{L}^{-1}$  after 170 days. In contrast, leaching from both the substrate controls and the substrate-litter treatments was significantly lower throughout the whole experimental period with mean concentrations  $< 1.6 \text{ mg K}^+ \text{L}^{-1}$  indicating that litter-derived  $K^+$  was strongly retained in the soils. The addition of litter material resulted in a respiration flush due to easily available organic substances at the beginning of the experiment. *L. corniculatus* litter with low C/N ratio is decomposed much faster compared to *C. epigejos*.

At the start of the experiment start short-term maximum  $\text{CO}_2$  emissions were recorded for the loamy sand treated with *L. corniculatus* litter. But long-term pure sand with *C. epigejos* litter had highest  $\text{CO}_2$  emission rates. That corresponds to the results of the experiment at the experimental field site together with subproject B3. Shifts in microbial communities were measured. Within the first 15 weeks strong decomposition of *L. corniculatus* was observed. That changed after 30 weeks to preferred degradation of *C. epigejos*. DOC and total dissolved nitrogen (TDN) leaching were strongly influenced by substrate texture and litter quality. DOC leaching was much higher from sandy than from loamy substrate. Additional information on the transformation and fate of litter-derived C is expected from  $\delta^{13}\text{C}$ -analyses of gas, percolate and solid samples which. First results from isotope analyses of DOC within the first 14 weeks indicate highest leaching of litter-derived DOC for the pure sand, particular for the *C. epigejos* treatment that was two times higher compared to *L. corniculatus* (Fig. 3).

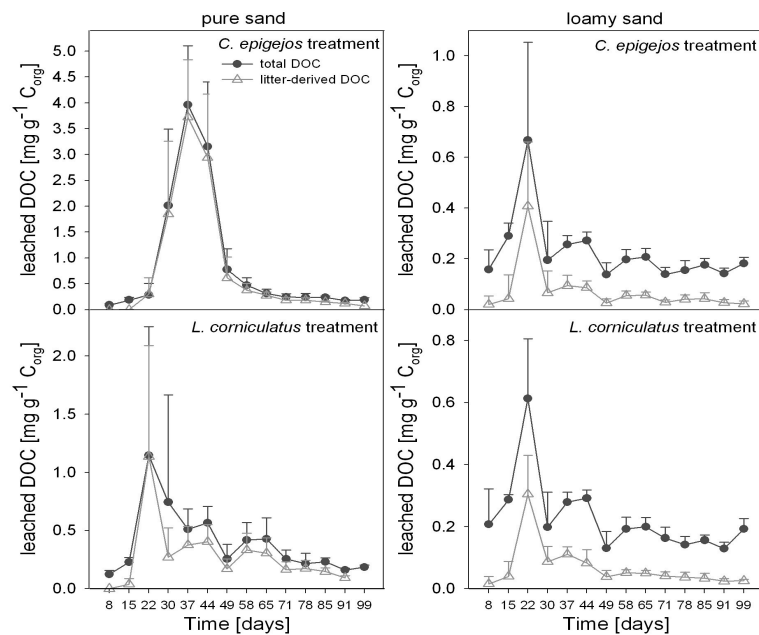


Fig. 3: Leached amounts of DOC from the microcosm columns. Litter derived DOC was calculated from  $\delta^{13}\text{C}$ -analyzes.

Significant leaching of soil-derived DOC was observed only for loamy sands. TDN leaching and nitrification were constrained to treatments with litter of *L. corniculatus* (Fig. 2b). The maximum TDN concentrations were higher and earlier for the loamy sand (max.  $50 \text{ mg L}^{-1}$  after 60 days) compared to pure sand (max.  $32 \text{ mg L}^{-1}$  after 100 days).

By including litter from two types of plant species with wide distribution within the catchment and two soil substrates representing the main textural variation types of the sediments used for catchment construction we are able to characterize the general function of these sub-patches in the catchment with respect to litter decomposition, soil solution composition, DOC and nutrient leaching, and impact on the mineral phase. The results suggest that initial differences in substrate composition in combination with invading vegetation leads to the development of patterns with different biogeochemical process intensities within the catchment. These patterns are not mere additive effects of substrates plus litter, but reflect differences in element cycling.

## 2.2 C flux measurements at the Damma and Chicken Creek sites

The main objective of the C flux measurements was to estimate the effect of initial soil development on the pathways of soil C cycling. At the forefield of the Damma glacier, pools and fluxes of C and N but also other soil characteristics such as texture, mineralogy, cation exchange capacity, and major cations were measured at 24 sites of four classes of soil ages: 2-18 years, 60 to 80 years, 110 to 130 years, and above 360 years. Here, we collaborated with the ETH project BIGLINK and the subproject A3 (Bernasconi et al., 2011).

In addition, soil CO<sub>2</sub> effluxes and DOC leaching have been measured bi-weekly throughout two growing seasons. The weathering status of the soils as indicated by the ratio of aluminium to the sum of major cations was close to the bedrock (0.5) along the whole chronosequence even at the 120 year old sites (0.57). This indicates that soils have undergone only a small degree of chemical weathering during 150 years. Along the glacier forefield, there has been a build-up of soil C by approximately 50 g C m<sup>-2</sup> y<sup>-1</sup>. However, the increase in soil C was not continuous. Soil C contents decreased in between the age classes, very likely due the addition of fresh sediments during the glacier re-advance and, thus SOC contents diluted to values similar to the newly exposed samples. Age estimates of SOM showed an unexpected result. Mean radiocarbon of the ‘youngest’ soils were more than 2000 year old, indicating that fossil soil C or C from aerosols contributed substantially to the initial soil C and thus, also the initial C fluxes. Both soil CO<sub>2</sub> effluxes and DOC leaching rates increased concomitantly to soil C stocks. While respiration was about six times higher at the 120 year old sites than at the 10 year old sites, DOC leaching was 20-40 times in the older soils. The annual soil CO<sub>2</sub> effluxes at the 120 year old site amounted approximately to 300 g C m<sup>-2</sup> y<sup>-1</sup>. Consequently, the annual fluxes were much higher than the accumulation rates of soil C, showing that only a small portion of the soil C cycling is sequestered in the soil. In the growing season 2010, soil respiration was separated into its autotrophic and heterotrophic component with a ‘vegetation removal experiment’. Moreover, we determined the radiocarbon ages of soil-respired and leached DOC, which will give us additional insight into the development of soil C cycling with increasing soil genesis.

At the Chicken Creek site, the soil CO<sub>2</sub> effluxes were measured in six measurement campaigns. As expected, the rates were relatively low (mean: 33 ± 4 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup>), but higher as at the 10 year old site at the forefield of the Damma glacier. The soil respiration rates showed a clear seasonal pattern and a gradient within the catchment with the rates decreasing down the slope.

### **2.3 Labeled litter experiment at the Damma glacier forefield**

To identify the fate, the turnover and the transformation of new litter C and old SOM in different soil ages isotopically labelled litter (2.5 g *Leucanthemopsis alpina*, <sup>13</sup>C +110 ‰ and <sup>15</sup>N +900 ‰) was added to soil columns along the chronosequence (10 yr, 70 yr, 120 yr) at the Damma Glacier forefield (Gülland et al., 2012, 2013). In collaboration with subproject B3, the litter-derived CO<sub>2</sub>-efflux, DOC leaching at 10 cm soil depth, and microbial C was followed throughout the snow-free season. Results showed a rapid mineralization flush at the beginning of the litter addition, while the leaching of litter DOC peaked two weeks later. Overall, the major fraction of the litter was lost via respiration (40-50 % of initial litter), while only 0.5 to 1 % were leached as DOC.

Soil age did not affect the mineralization rate of the litter, but litter-derived DOC leaching decreased significantly with soil age. The stronger retention of DOC in the older soil can very likely be attributed to higher interaction of DOC with the mineral surfaces because weathering and thus, reactivity of the surfaces increased with increasing age.

## 2.4 Geostatistical sampling

A first geostatistical sampling was carried out in 2008 as a base for characterizing surface soil development. 192 plots were sampled within the catchment along a grid representing 7 distance classes (Fig. 4). Samples were taken from 0-3 cm depth since we expected earliest signs of soil formation in the top soil. Samples were analyzed for texture, bulk density, water content, pH,  $C_{org}$ , total element contents, pedogenic oxides and hydroxides, soluble phosphor,  $\delta^{13}C$  of organic and inorganic C, and microbial DNA in a joint effort of subprojects A2, A3, B1, B3, and C5. In addition, photos of all 192 sampling plots were taken for documentation.

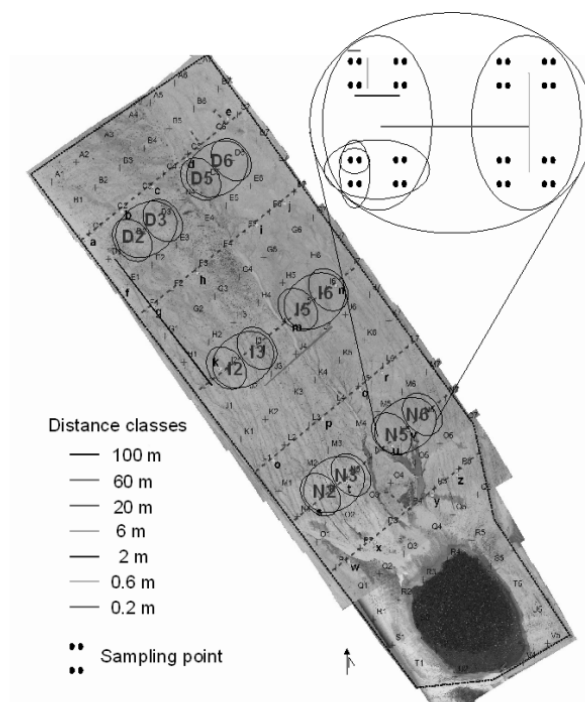


Fig. 4: Design of the geostatistical sampling in 2008 with 12 central points and 7 distance classes.

Beside the initial contrast in texture between the SW and NE part of the catchment, all variables, except for the coarse sand content, were spatially auto-correlated and all variables (except coarse sand content) showed an increase of the spatial variation up to distances of at least 2 m (Papritz et al., 2010). Developing structures like erosion gullies affect soil chemical properties particularly with regard to organic carbon ( $C_{org}$ ). Samples from within erosion gullies showed significantly lower  $C_{org}$  contents compared to adjacent sampling points especially in still active gullies indicating erosion induced  $C_{org}$  losses.

Samples were also used as reference in the investigations of subproject A3 to study soil formation processes in biological soil crusts (Fischer et al., 2010). Results of the top soil characterization were also provided to subproject C5 for the development of the structure and process model.

In 2011, the grid sampling was repeated with the same design and parameters by subprojects A2 and A3. Images of sampling points were analyzed using Adobe Photoshop for plant cover including plant litter. In 2008, 60 % of the samples showed a plant cover < 5 % and only 14 % > 20 % (Fig. 5). Three years later, plant cover was significantly increased with only 8 % of the samples with values < 5 % and 83 % with a plant cover > 20 %, corresponding to the results of the overall vegetation monitoring in the catchment (Zaplata et al., 2011).  $C_{org}$  contents were correlated to plant cover and were substantially increased from  $0.19 \pm 0.11$  % in 2008 to  $0.61 \pm 0.37$  % in the 2011 samples (Fig. 6).

## 2.5 Soil microbial activity at Chicken Creek

Soil samples were taken at 0-3 cm and 3-10 cm depths along the established grids lines D, I, N and around the pond (RS) in August 2011. Soil microbial respiratory activity was estimated by the Sapromat respirometer (Dilly et al., 2008). Microbial biomass carbon was estimated after glucose addition to induce maximal initial respiratory response (Anderson & Domsch, 1978).

Basal respiration and  $C_{mic}$  at the 0-3 cm soil depth increased from the upper part ( $0.18 \mu\text{g CO}_2\text{-C mg}^{-1} \text{ soil h}^{-1}$  and  $65 \mu\text{g C}_{mic} \text{ g}^{-1} \text{ soil}$ ) to the lower part ( $0.46 \mu\text{g CO}_2\text{-C mg}^{-1} \text{ soil h}^{-1}$  and  $176 \mu\text{g C}_{mic} \text{ g}^{-1} \text{ soil}$ ) of the catchment (Fig. 5). Both BAS and  $C_{mic}$  at the top 3 cm soil depth were significantly highest at the vicinity of the pond in the lower part of the catchment (Fig. 7). This pattern may have been derived from more readily available carbon, and also by translocation towards lower parts of the catchment. In contrast, BAS and  $C_{mic}$  at the 3-10 cm depth varied spatially and were not significantly different among grids. The microbial indicators provide insight into the status of the initial soils across the catchment, and reflected soils in early stages of development with an enhanced microbial biomass (particularly around the pond) constituting a considerable proportion of organic matter accreted in this initial system.



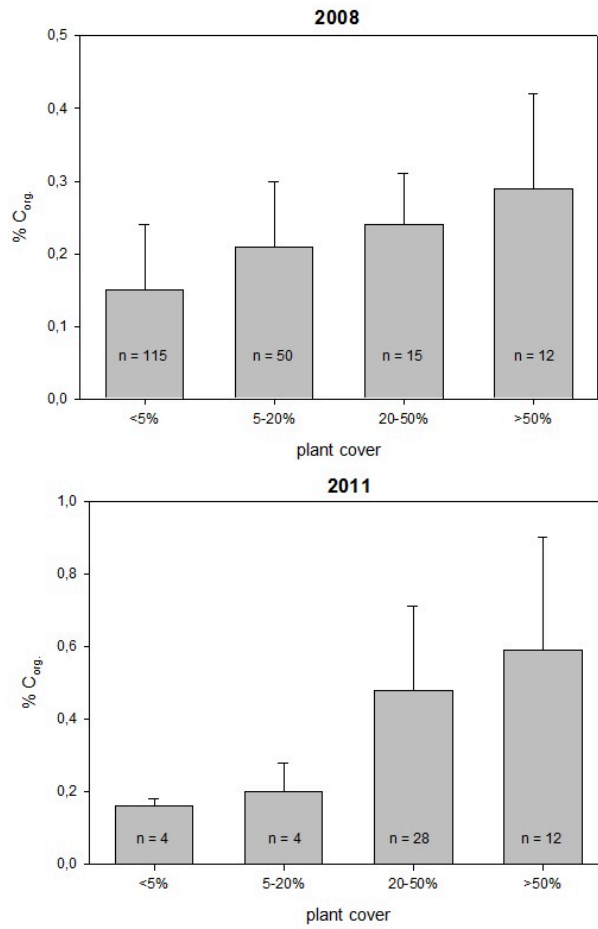


Fig. 5: Distribution of plant cover and C<sub>org</sub> contents in grid samples (0-3 cm) in 2008 and 2011.

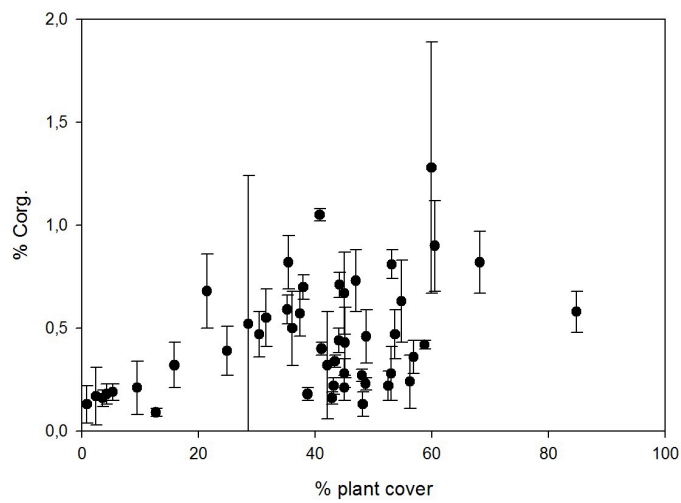


Fig. 6: Correlation between plant cover and C<sub>org</sub> contents in the grid samples of 2011.

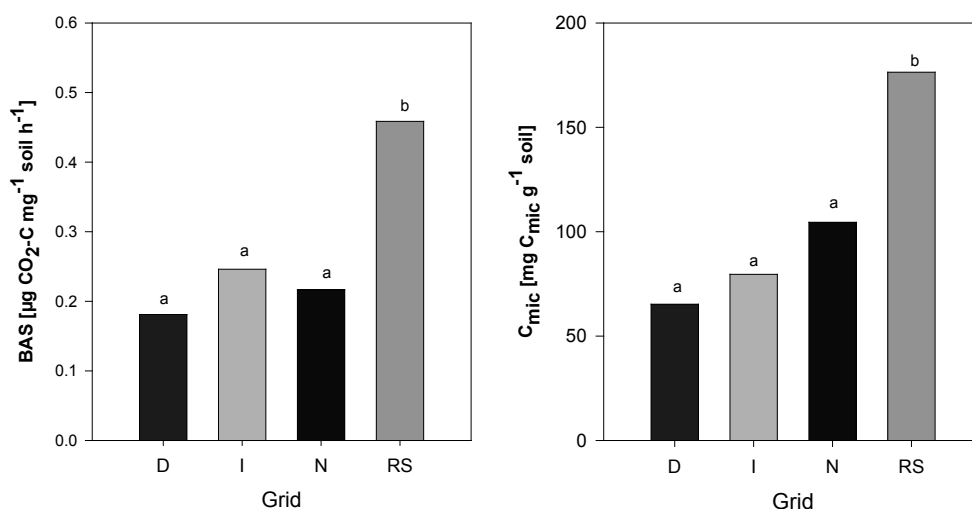


Fig. 7: Soil microbial basal respiration (BAS) and microbial biomass ( $C_{\text{mic}}$ ) at the 0-3 cm depth along grids across the catchment (different letters indicate significant difference (n=8), Holm-Sidak,  $P < 0.05$ ).

## 2.6 Additional activities

Mineral soil crusts which were observed mainly during summer in the catchment were sampled and characterized. Whitish precipitations along the walls of erosion gullies were identified as  $\text{CaSO}_4$  crusts. White crusts at the soil surface observed in large areas in the lower part of the catchment could also be identified as gypsum precipitations.

Organic carbon in the substrate of the catchment as well as DOC from different flow paths was dated using the  $^{14}\text{C}$  method.  $C_{\text{org}}$  of the sediment showed  $^{14}\text{C}$  ages between 3,000 and 15,000 years indicating that the initial C content of the substrate is fossil, but most probably not influenced by lignite derived C from the mining activities. The DOC had  $^{14}\text{C}$  ages of around 2,800 years indicating a significant contribution of fossil C to DOC transport within and export from the catchment.

To elucidate the bioavailability of this old DOC along hydrological pathways in the catchment a joint experiment with subprojects A3, B3 and B5 was started. DOC was sampled in soil solution, groundwater, stream and lake water and inoculated crosswise with samples from the different sites. Results indicating low bioavailability of the old DOC have been published by Risse-Buhl et al., 2013.

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## **Project A3 – Initial stages of humus development**

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### **1 Introduction**

The major research question of A3 concerns processes and structures that control soil formation and humus accumulation in the initial phase of ecosystem development. We had hypothesized that in the initial stage of terrestrial soil organic matter (SOM) formation the development of hydrophobic surfaces and biocrusts as well as the selective accumulation of recalcitrant organic matter are the dominating mechanisms. These processes, which are highly affected by the development and succession of pioneer vegetation, will result in different soil structures which in turn influence the water and element budget on catchment level.

The sites analyzed for patterns and processes of SOM formation in the first phase were

- the Dammaglaciar chronosequence
- artificial sand dunes at “Lugteich”
- natural sand dunes at “Lieberose”
- the “Chicken Creek” catchment

The analysis of patterns and processes of SOM formation in the initial phase of soil development was focused on the chronosequence at the Damma glacier forefield (Switzerland). The development and chemical composition of biological soil crusts (BSC) as carbon source and their effects on the mineral substrate in initial ecosystems was investigated at the artificial “Lugteich” and natural “Lieberose” sand dunes. The proposed analysis of a chronosequence on sandy substrates in Brandenburg could not be realized as the sand dunes available for sampling did not show the age distribution expected and necessary for the investigation of the initial phase of SOM formation. In order to investigate the soil formation in the Chicken Creek catchment, a geostatistical sampling of the topmost soil material (0-3 cm) was initiated together with projects A2, A4, B1 and B4 in 2008. A balanced nested sampling design was applied which included 192 locations and seven spatial scales from 0.2 to > 60 m to assess the initial distribution of physical and chemical soil properties (the detailed sampling design is found in Papritz et al., 2010). This sampling campaign of the Chicken Creek catchment was repeated in 2011 inclusive of additional sampling sites with robinia trees and sea buckthorn.

## 2 Results

### 2.1 Chronosequence glacier forefield

The proglacial area of the Damma glacier offers a time sequence from three classes of surface age (ca. 15 yrs, 60-80 yrs, 110-140 yrs). Mature soils outside the proglacial area are older than 700 years and serve as reference for advanced soil development. Twenty-two soils (3 replicates) were investigated in the Damma glacier forefield to assess the build-up of organic matter stocks in mineral soils and organic surface layers with increasing ice-free period. The soils developed on granitic parent material comprise Leptosols and Regosols in the forefield, and Cambisols outside the proglacial area. Glacial deposits and subsequent glaciofluvial erosion produced a heterogeneous and small-scale pattern of soil development stages within the same age class concerning the formation of Ah horizons and organic surface layers, texture and the accumulation of SOM and non-crystalline Fe and Al phases. Despite of this additional gradient in soil age, mean values for soil age classes showed rapid above- and belowground organic carbon accumulation (Dümig et al., 2011). The mean annual accumulation rate of SOC ( $7.1 \text{ g m}^{-2}$ ) and the total pool of pedogenic Fe and Al ( $0.4 \text{ g Fe}_d + \text{Al}_o \text{ m}^{-2}$ ) of the glacier forefield soils are higher when compared to those of the oldest foreland soils (110-140 yrs) to the mature soils ( $> 700 \text{ yrs}$ ) with  $3.1 \text{ g SOC m}^{-2}$  and  $0.2 \text{ g (Fe}_d + \text{Al}_o) \text{ m}^{-2}$ , respectively. This indicates that the slowdown of accumulation of OC, non-crystalline Fe oxides and Al phases starts already after some hundred years of soil formation. The strong correlation between SOC and oxalate soluble Fe and Al indicates that the storage of organic carbon during initial pedogenesis is mainly controlled by the formation and accumulation of ferrihydrite and poorly crystalline Al phases (Dümig et al., 2011).

The OM loading of the clay fractions increases from  $44 \text{ mg g}^{-1}$  in the young soils to  $190 \text{ mg g}^{-1}$  in the 110-140 year old soils and to  $323 \text{ mg g}^{-1}$  in the mature soils (Dümig et al., 2012). This leads to decreasing specific surface areas of the clay fraction as determined by  $\text{N}_2$ -adsorption (BET approach). The clay fraction minerals are dominated by illite, irregularly interstratified mica/vermiculite, and ferrihydrite. A strong correlation is found between increasing ferrihydrite contents (determined as oxalate-soluble iron) and increasing OM contents of the clay fraction with soil formation. This implies a major role of ferrihydrite for the stabilization of OM during initial soil formation (Dümig et al., 2012). The progressive OM loading of the clay fraction with increasing soil age results in higher sorption capacities as shown by the strong correlation between OM content and potential cation exchange capacity, which is in line with XRD analysis. Solid-state  $^{13}\text{C}$  NMR spectroscopy revealed the compositional changes of SOM in bulk soils as well as in clay fractions. The increase of O/N-alkyl and alkyl C with soil age is due to the specific accumulation of these components in the clay fraction, whereas the OM inherited from the glacial till is rich in aromatic and carboxyl C.



Formation of organo-mineral associations starts with the accumulation of O/N-alkyl C in the proglacial area, which is in line with hydrolysable neutral sugar and amino acid contents of the clay fractions. Accumulation of alkyl C is detected at a later stage only in the mature soils. This is associated with a change in the C/N ratio of the clay fraction from 10 in the proglacial area to 13 in the mature soils. The sequential accumulation of different organic compounds and the large OC loadings point to multiple accretion of OM in distinct zones or layers during the initial evolution of clay fractions (Dümig et al., 2012).

In summary, initial soil formation and SOM accumulation after glacier retreat is surprisingly fast. The accumulation of SOM in the clay fraction of these soils is controlled by weathering and formation of ferrihydrite, which in turn leads to a specific accumulation of O/N alkyl C compounds during initial soil formation (Dümig et al., 2012). Egli et al. (2010) found similar results with respect to the formation of organo-mineral associations, and claimed that this process “has existed since the very beginning of soil formation”. In contrast, our results suggest that mineral weathering and the formation of ferrihydrite is a prerequisite for substantial accumulation of organo-mineral associations. At the Dammaglacier forefield this becomes evident in the soils after 60 years of soil development, whereby mineral weathering and OM accumulation proceed in different timescales (Dümig et al., 2012).

## 2.2 Biological soil crusts

Biological soil crusts (BSC) were investigated in artificial (Lugteich) and natural (Lieberose) dune systems, to elucidate their role as carbon source in initial ecosystems. The sand dunes showed substrates with similar physical properties. Bulk densities (0-3 cm) varied between 1.4-1.6 g cm<sup>-3</sup> and 1.5-1.7 g cm<sup>-3</sup> at the natural and artificial sand dune, respectively. As expected, both sand dunes showed low portions of the particle-size fraction < 63 µm with a maximum of 2.7 mass-%. In most BSCs the portions of the fraction < 63 µm was higher when compared to the corresponding substrates. The artificial sand dune showed slightly higher portions of the fraction < 63 µm than the natural sand dune. The texture analyses of samples from the artificial sand dune revealed slightly higher silt and clay contents of BSCs when compared to the substrates which is in line with portions of the fraction < 63 µm. At both sand dunes, we found no difference of oxalate and DCB-extractable Al, Fe and Si between the development stages of BSCs. The artificial sand dune showed slightly higher Fe<sub>o</sub> and Fe<sub>d</sub> concentrations of BSCs and substrates when compared to those of the natural sand dune. pH values (H<sub>2</sub>O) of BSCs were also similar between the natural (5.0 ± 0.1) and artificial (5.1 ± 0.2) sand dune, and no marked changes were detected between the different development stages of BSC.

The substrates (bulk materials) similarly showed low OC contents ( $1.2 \pm 0.5 \text{ mg g}^{-1}$ ) below the different development stages of BSCs. In the contact zone with the mineral soil (2-3 mm) the organic carbon concentration is about threefold higher in BSCs as in the parent material. Thus, colonization of BSCs on bare substrate results in fast SOC accumulation in the upper first millimeters of the surface (artificial dune:  $2\text{-}7 \text{ mg g}^{-1}$  OC within three years). The range of BSC-derived OC input (OCBSC – OCsubstrate) was similar between the natural sand dune ( $0.8\text{-}9.6 \text{ mg g}^{-1}$ ) and artificial ( $1.9\text{-}9.3 \text{ mg g}^{-1}$ ) sand dune. However, OC inputs differed strongly in dependence of the BSC development stage and cyanobacteria-dominated BSC showed lower inputs of OC than BSCs with mosses.

BSCs showed a wide range of carbohydrate-C content for the different development stages at the natural ( $46\text{-}721 \text{ mg g}^{-1}$  OC) as well as artificial ( $323\text{-}597 \text{ mg g}^{-1}$  OC) sand dune. The change from initial substrate conditions to cyanobacteria-dominated BSCs, and to BSCs with the contribution of mosses was combined with strongly increasing carbohydrate-C contents. In the course of vegetation succession (pure BSC to moss mixed with BSC) a specific microbial carbohydrate signature is associated with the presence of biological soil crusts. Almost all BSCs had high ratios of galactose plus mannose over arabinose plus xylose (GM/AX) of  $> 2$  indicating the predominance of microbially-derived carbohydrates. The highest GM/AX ratios were found for initial substrate conditions and cyanobacteria-dominated BSCs without other vegetation in the vicinity of BSCs.

Microbial-derived carbohydrates, which represent up to 70 % of TOC, are the major OC input to the soil. This is in line with the relative proportions of O-alkyl C as determined by  $^{13}\text{C}$  NMR spectroscopy. In addition,  $^{13}\text{C}$  NMR spectra revealed that BSCs at the natural dune accumulate more O-alkyl C, but not alkyl C when compared to the artificial dune. BSC-derived OC mainly comprises O-alkyl C (carbohydrate-C), alkyl C and N-alkyl C in varying compositions indicating distinct BSC communities between natural and artificial dune. The crust type (e.g., cyanobacteria-dominated crust) does not depend on physical or chemical properties of the substrate (e.g., texture, pH), but rather on abiotic factors like microrelief and -climate (surface stability).

Due to the input of OC chemical weathering and formation of pedogenic minerals are accelerated, as shown by 10-30 % higher concentrations of oxalate and dithionite soluble Fe as compared to those of the parent substrate. The content of microbial-derived sugars of the BSC is correlated with increased water repellency of the sandy substrate. This in turn affects water infiltration and soil hydrology (see Fischer et al., 2010b). In the first phase of the project it was assumed that amount and quality of SOM influence soil structure as well as physical soil properties. In particular water repellency, which was considered to be a significant component in soil hydrology, may be determined by non-polar organic compounds, which contribute only a small proportion of OM to the total pool of SOM.

Weak correlations have been reported in the literature between degree/persistence of water repellency and SOM contents, most likely due to structural effects like coating of soil particles with (I) aliphatic hydrocarbons and (II) natural surfactants. Both types bind to charged surfaces with their hydrophilic head creating a non-charged, hydrophobic surface with their hydrophobic tails, which are directed towards the soil solution. Fourier transformed infrared (FTIR) microscopy was considered to facilitate the non-destructive investigation of hydrophobic surfaces on a microscale level. Modeling of water budgets on a catchment level may be hindered if the occurrence of water repellency is not considered.

It was found that (BSC) appeared rapidly on bare mineral substrate, and that these BSCs influenced the water flows by means of:

(I) Water repellency

Traditional methods, like contact angle (CA) or water drop penetration time tests (WDPT) require pronounced repellency, where delayed wetting of the surface permits the measurements. Throughout the period of investigation at Chicken Creek, wetting occurred immediately, and it was necessary to adapt other methods, which respond to surface polarity and which are applicable under these conditions. We found that repellency indices (RI) increased with the development of BSCs, and decreased as mosses superseded cyanobacteria (Fischer et al., 2010b).

(II) Pore clogging

The swelling of microbial mucilage of BSCs upon wetting caused a decrease of water infiltration (Fischer et al., 2010b).

(III) Water holding capacity (WHC)

The WHC correlated closely with SOM storage and increased with crust development. Better water availability, however, exposes surface microphytes to the risk of replacement by higher vegetation during plant succession under temperate conditions. A mechanism of crust stabilization was proposed where BSCs benefit from increased texture and biomass mediated water supply, and where the water supply to higher plants was limited due to alteration of physico-chemical surface properties (repellency, “wettability”). It is hypothesized that only BSCs able to prevent usage of water by higher plants may stabilize under temperate conditions (Fischer et al., 2012a).

(IV) Mineral particle and pore space orientation

We have indication that stratification and horizontal orientation of particles and pores may act as a physical infiltration barrier. We found that the improved water availability in fine-textured crusts may promote settlement and development of BSCs (Fischer et al., 2012a).

## (V) Collection of Dew

The suggested mechanism of dew formation involves a delay in water saturation in near-surface soil pores and extracellular polymeric substances (EPS) where the crusts were thicker and where the water capacity was high, resulting in elevated vapor flux towards the surface. It was also found that the amount of dewfall was too low to observe water flow into deeper soil. Analysis of the soil water retention curves revealed that, despite the sandy mineral matrix, moist crusts with clogged by swollen EPS pores exhibited a clay-like behavior. It is hypothesized that BSCs gain double benefit from suppressing their competitors by runoff generation and from improving their water supply by dew collection. Despite higher amounts of dew, the water availability to the crust community decreases with crust development, which may be compensated by ecophysiological adaptation of crust organisms, and which may further suppress higher vegetation or mosses (Fischer et al., 2012c).

It was also found that the geomorphological differentiation was related to crust development, where substrate dependent water availability defined the crust type. On a catena along an artificial dune, the establishment of the biological soil crusts was closely associated with the vegetation succession, whereas no clear succession of the crusts could be observed at Chicken Creek. The mosaic-like pattern of the biological soils crusts was associated with the distribution of fine-grained material here (Spröte et al., 2010a). We further propose and discuss three stages of N process succession. First, the heterotrophic stage (mobile sand without BSCs) is dominated by mineralisation activity. Second, during the transition stage (initial BSCs), N accumulates, and potential nitrification and denitrification activity increases. Third, the developed stage (established BSCs and reference) is characterised by the dominance of nitrification (Brankatschk et al., 2012).

A new method for high resolution imaging of Normalized Difference Vegetation Indices (NDVI) of BSCs was developed (Fischer et al., 2012b). The NDVI is well correlated with various vegetation parameters, such as green biomass (Tucker, 1979), chlorophyll concentration (Buschmann & Nagel, 1993), leaf area index (Asrar et al., 1984), Karnieli & Tsoar (1995) and Karnieli et al. (1996) tested whether high NDVI values may be caused by the photosynthetic activity of BSCs. A high correlation was reported between NDVI values and chlorophyll content of a wet BSC (Karnieli et al., 2001). The new method promises to facilitate field measurements of NDVIs at a scale, which is not accessible by remote sensing or by field portable spectrometers. Perspectively, it may also be used for field monitoring of biological soil crusts or vascular vegetation, and for relating the spatial distribution of BSCs to hydrological or pedological surface patterns.

In conjunction with traditional wet chemical analyses, scanning electron microscopy (SEM), x-ray fluorescence analysis (EDX) and FTIR microscopy were successfully utilized to study initial pedogenesis in BSCs. It was found that exopolysaccharides, originating from BSCs, promote trapping of sediments. Weathering of carbonates combined with a drop in pH occurred within the first years of development, but were limited to the upper millimeters of the soil profile. Further, the lower part of the crust was stabilized by organo-mineral compounds, which accumulated in the contact zones of sandy particles. FTIR microscopy pointed to the fossile origin of OM involved in this stabilization (Fischer et al., 2010a).

WDPT and CA measurements were conducted at older reference sites, where water repellency was more pronounced. There, water repellency strictly depended on the age of Scots pine stands (Spröte et al., 2010b). We attribute this observation to cuticular waxes on pine needles and in litter. LC, GC and FTIR measurements of pine needle, litter and soil are ongoing.

The particular significance of BSCs for water flows points to the relation of our experiments with the projects A2 (Interactions between soil solution and mineral surfaces), A4 (Development and interactions of flow paths on the surface and in the soil) and Z1 (Monitoring and Site Management). Due to shading or the development of organic soil horizons, BSCs disappear under vascular plant cover. The interaction between BSCs and vascular plants will be studied in further projects.

In the catchment "Chicken creek", the substrate at the soil surface (0-3 cm depth) shows a wide spectrum of physical (texture, bulk density, rock fragments) and chemical (oxalate and dithionite extractable Fe, Al and Si) properties. For example, clay contents and dithionite soluble Fe of the 192 sampling spots show values of 0-39 % and 0.7-5.3 mg g<sup>-1</sup>, respectively. These initial heterogeneities and spatial structures result from the construction process (Papritz et al., 2010). Higher clay contents are associated with higher OC contents, which are most probably inherited from the parent substrate. Consequently, DOC obtained from two different groundwater samplers shows a high radiocarbon age (A2), and high aromaticity (<sup>13</sup>C NMR spectroscopy). When compared to the bare substrate, accumulation of new OM could not be detected in 2008, not even at locations where vegetation was established within three years of system development. The comparison between the sampling in 2008 and 2011 showed significantly higher OC concentrations in almost all samples from 2011. We found a mean OC accumulation of 3 mg g<sup>-1</sup> ± 3 (maximum of 19 mg g<sup>-1</sup>) after six years of soil development. Further, OC content is related to the content of particulate organic matter as well as plant cover. Soil acidification is also proceeding as samples from 2011 showed significantly lower pH<sub>H<sub>2</sub>O</sub> values when compared to those of 2001 (mean decrease of pH<sub>H<sub>2</sub>O</sub>: 0.5 ± 0.3). In contrast, no change was detected for concentrations of oxalate- and DCB-extractable Fe, Al, Mn and Si for almost all samples.

When compared to adjacent soils without trees or shrubs, topsoils under robinia trees and sea buckthorn which were sampled in 2011 were not enriched in organic matter. There, organic matter still accumulates in organic surface layers without noticeable incorporation or translocation into the mineral soil. The mean OC stocks of organic surface layers amounted to  $126 \pm 37 \text{ g m}^{-2}$  under robinia and  $196 \pm 59 \text{ g m}^{-2}$  under sea buckthorn.

For the eastern and western parts of the upper slope of the Chicken Creek catchment, three phases of BSC cover development could be distinguished:

- (I) Phase of initial BSCs and BSC establishment, starting from installation of the monitoring plots and lasting to spring 2009.
- (II) Burst of higher vegetation in summer 2009, which is in accordance with the findings of Zaplata et al. (2011) who reported a preliminary maximum of the mean total vascular vegetation cover amounting to  $38.5 \pm 4.3 \%$  for 2009.
- (III) Establishment of relative dense vegetation, where mosses and higher vegetation covered most of the surface.

The southern downslope area of the catchment generally followed this pattern, with the exception that the surface cover development was delayed compared with the eastern and western upper slope part and that there was no burst in higher vegetation in summer 2009.

These stages of surface cover development were clearly related to surface patterns. Flow channels initially formed on the bare substrate pre-defined algal crust cover patterns, which disappeared when replaced and when flow channels were occupied by mosses and higher vegetation. In addition, algal crust patches pre-defined growth-patterns of higher plants.

The mean value of the repellency index of the substrate amounted to  $1.1 \pm 0.3$  which is close to the theoretical value of 1 for a totally non-repellent soil (Hallet & Young, 1999). Repellency indices amounted to  $1.6 \pm 0.4$  and  $1.8 \pm 0.4$  for weak BSCs and for the mostly crusted surface, respectively. Because repellency indices will exceed a value of 50 for highly repellent soils (Urbanek et al., 2007) and exceed values of 8 on *Zygonium*-dominated natural inland dunes of the region (Fischer et al., 2010b; 2012b), water repellency has to be characterized as low throughout the monitoring period.

Although algal crusts inhibited infiltration (Spröte et al., 2010a and b), it can be concluded that BSCs did not stabilize in the Chicken Creek catchment. BSC development followed the patterns of water availability, which differed between the eastern, western and southern parts of the experimental site. In addition to high precipitation, low water repellency and improvement of water availability in BSCs promoted the establishment of mosses and higher plants.

Under the given conditions, the crusted period of the Chicken Creek catchment represented a transitional phase during early ecosystem development, which started 2-3 years after installation and which lasted less than two years before BSC replacement.

### **3 Conclusions**

From the perspective of soil development, we found several similarities between the man-made landscape at "Chicken creek" and newly formed land surfaces following deglaciation. Both ecosystems are characterized by the presence of organic carbon inherited from the parent material, which represents an important microbial OC source at the start of ecosystem development (Bardgett et al., 2007). Chemical weathering and the formation of iron oxides is triggered by OC input in the submicron contact zone with BSC in the very early stages of soil development. These iron oxides are the major mineral surfaces, where SOM accumulation and formation of organo-mineral associations occur.

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## **Project A4 – Development and interactions of flow paths on the surface and in the soil**

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### **1 Introduction**

Flow paths on the soil surface have been described using fractals (among other approaches) for larger catchments (e.g., Caylor et al., 2005). For agricultural field soils, surface flow paths were studied using irrigation experiments and laser scanning of the micro topography (e.g., Römken et al., 2002). Similar rain simulators were used to describe the surface structure dynamics in shrinking soils. A feedback between plant growth, reduced runoff, and increased infiltration was postulated for semiarid areas with patchy vegetation (Ludwig et al., 2005). Formation of surface crusts changes the hydraulic properties of the soil surface layer (Assouline, 2004). Flow paths are analyzed using tracer experiments in combination with image analysis and numerical modeling (e.g., Gerke et al., 2009; 2010). Quantification of preferential flow at field scale or during snow-melt and frozen soil conditions is largely unresolved; the use of non-intrusive and continuous monitoring methods and techniques for studying flow inside macropores and along the macropore walls is lacking (Allaire et al., 2009). Flow paths and soil moisture may be identified with distributed temperature sensors (DTS) systems (e.g., Steele-Dunne et al., 2010).

For studying interactions between surface runoff and infiltration, the St. Venant equation was coupled with an approach for infiltration into macroporous soils by including surface micro-topography (e.g., Ruan & Illangasekare, 1998). The spatial distribution of macropores controlled infiltration and surface runoff by local water supply of macropores and by the structure “building” capabilities of earthworms and termites (e.g., Leonard et al., 2004). Soil organisms (e.g., Langmaack et al., 2001) and plant roots (e.g., Whalley et al., 2005; Scanlan & Hinz, 2010) can strongly change soil hydraulic and mechanic properties. In hydrology, initialization of macropore infiltration was found highly sensitive for triggering preferential flow (Weiler, 2005). By introducing a mixing cell at the soil surface, solutes and pesticides were distributed in fractions of matrix and macropore infiltration and depending on rain characteristics (McGrath et al., 2008). At the upper boundary, a domain-specific distribution of infiltration has to be considered (Dusek et al., 2008). Mechanic-hydraulic feedbacks were assumed for explaining particle mobilization by differential capillary stress from pore walls (Michel et al., 2010).

The finite difference-based MODHMS code coupled 1D/2D surface flow with 3D soil water flow equations (Panday & Huyakorn, 2004). The PSRM\_2D code coupled plot-scale water erosion with Green-Ampt infiltration (Nord & Esteves, 2005). Analytical descriptions of runoff and erosion distinguished between early and late times during individual events (e.g., Parlange et al., 1999). Effective hydraulic parameters were used for characterizing plot scale properties (Bayer et al., 2005).

For systems in the initial development phases, structural changes and feedbacks were expected to be highly dynamic and occurring at different scales. Major challenges and adopt and develop complex methods to quantify the flow paths and conceptually analyze the observations. The structural dynamics at the soil surface has important influence on erosion, infiltration, matter dynamics, and vegetation establishment among other processes. However, the initial soil structure formation at the surface is highly dynamic and spatially variable such that the knowledge is still limited.

## **2 Results and methodological development**

The first project period focussed on methodological development of (i) plot-scale irrigation-infiltration-runoff (and tracer) experiments for differently developed soil surfaces (at the Experimental Area on sandy substrates) and (ii) on the characterization and quantification of pore and hydraulic properties of surface soil layers using infiltrometer, X-ray CT, and neutron radiography techniques. The irrigation experiments are currently simulated using standard soil hydraulic model and a coupled 2D surface- and 3D subsurface flow model (Panday & Huyakorn, 2004, see above).

### **2.1 Field-plot irrigation-infiltration-runoff-erosion system**

The major methodological result is the development and test of a field-plot irrigation-infiltration-runoff-erosion system that combines erosion with methods from hydrological studies in an integrated experiment (Biemelt et al., 2009). This measurement system allows controlling most relevant parameters and driving forces to characterize the irrigation (spatial distribution, intensity and droplet energy and distribution), the surface flow (elevation model, micro-topography, flow field), the subsurface flow (tensiometer and dye tracing, 2D spatial flow path images), the runoff (flow velocities, sediment concentration) and sediment mass relocation. A number of modules had to be developed and optimized separately (e.g., sprinkler heads (FullJet instead of VeeJet), the characteristic droplet spectra of natural precipitation (Parsivel), imaging of surface flow velocities using a high resolution camera during the irrigation experiment and dye staining, and tensiometers and fluorescence tracer). Infiltrometer tests and soil sampling was carried out before and after the irrigation.

The irrigation experiment 3 was carried out 9 months after the experiment 2 on the same plot where the initially bare soil surface had changed in a way that was somewhat comparable to the development of soil surfaces in the Chicken Creek Catchment between 2005 and 2006. The resulting runoff and infiltration characteristics had changed after the winter (although no vegetation was visible then); runoff and sediment loss increased as compared to previous situation (Fig. 1). When analyzing the experiment within the 20 min irrigation time in detail (Fig. 1, right), the results demonstrate effects of changing surface structure on the infiltration-runoff ratio and the sediment yield. Currently, the results are simulated using the ModHMS code, coupling 3D-soil water flow with 2D surface runoff. The 2D spatial distribution array of irrigation was determined using Kriging. Soil hydraulic parameters were obtained from lab core measurements.

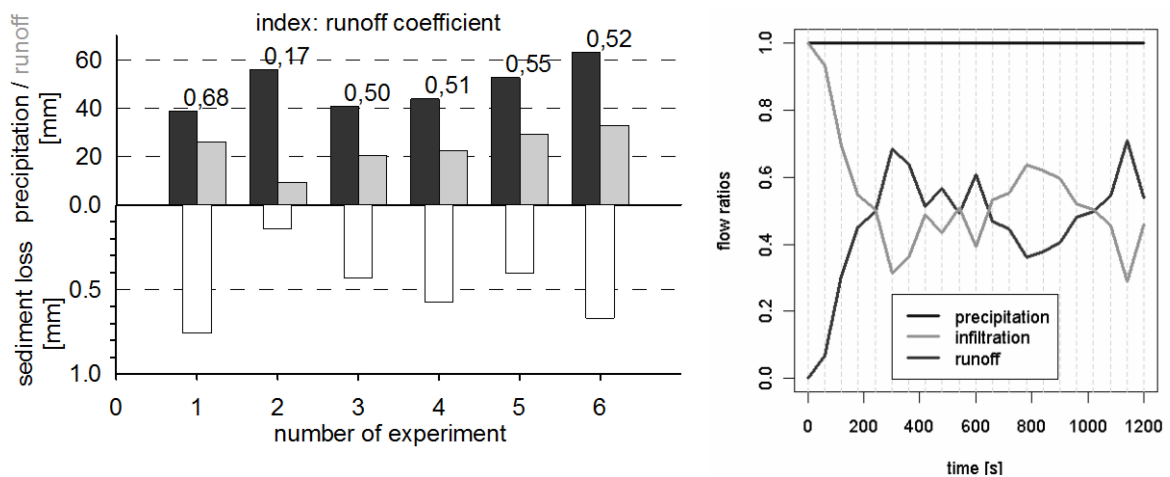


Fig. 1: Comparison of precipitation, runoff, and sediment loss from the 6 irrigation experiments (left) and time course of exp. 3 (right): (1) plane surface (PS) without vegetation (NOVEG), more silty surface sediments, 18.9.08, (2) PS, NOVEG, sandy surface, 23.10.08, (3) PS, NOVEG, some crust same sandy surface as (2), 16.7.09, (4) PS with a rill, NOVEG, partly crusted, sandy surface, 30.7.09, (5) small rill system, tree seedling, sandy surface partly crusted, 24.9.09, (6) intense rill system, some grass, sandy surface partly crusted, 30.9.09.

Since the field experiments showed obvious changes in runoff rates caused by small changes in surface structure, sensitivity analyses are carried out to test effects of soil surface parameter changes on changes in flow rates using the coupled 2D/3D ModHMS code. The ModHMS simulation results describe the tensiometer-measured soil wetting in principle during irrigation; however, the maximal saturation and the drying end of the curves are not fully matched (Fig. 2). The soil hydraulic parameters are currently also determined using inverse modelling with the HYDRUS\_1D code by analyzing the tensiometer data. Corresponding with field TDR and tensiometer observations, the simulation results indicate the importance of considering the hysteresis in the soil water retention function.

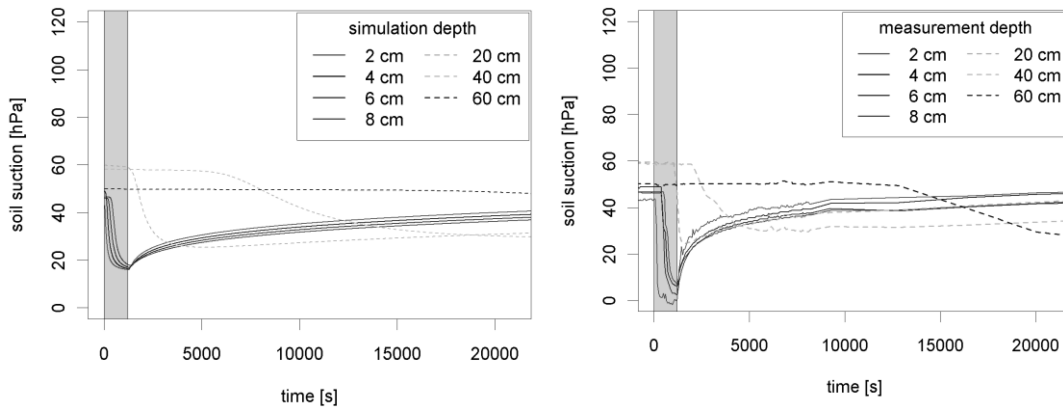


Fig. 2: Comparison between measured and simulated soil water tensions for the experiment 2.

After the irrigation experiments, soil blocks were analyzed and samples for bulk density (Exp. 3:  $1.7\text{-}1.8\text{ g cm}^{-3}$ ), water content ( $0.14\text{-}0.17\text{ cm}^{-3}$ ), particle size distribution, saturated hydraulic conductivity ( $170\text{-}240\text{ cm d}^{-1}$ ) and pictures of stained areas from dye tracers were taken to detect possible preferential flow paths along inclined soil layers.

## 2.2 Analysis of characteristic surface structures

The second aspect was the analysis of characteristic surface structures including crust formation. The aim was to observe and relate the structural formation of the top soil surface layers with hydraulic properties for three representative sites in the catchment. The ground-dwelling activity of pioneering ground beetle *Cylindera arenaria viennensis* (Schrank) modified the soil structure resulting in numerous vertical channels of about 1-2 mm in diameter and several centimeters in depth. The effect of these biopores on water infiltration and initializing preferential flow was analyzed using X-ray CT to identify the pore structure in combination with neutron radiography to quantify the flow patterns in and around the biopore (Badorreck et al., 2012).

Neutron radiography images revealed that unsaturated flow conditions created mainly uniform infiltration fronts within the first centimeters below the surface without burrows (i.e., initial surface condition) while burrows acted as preferential flow paths under relatively dry initial conditions. For one 3 cm surface soil core with a central burrow from a vegetation-free location near the pond, a denser upper, and a more loose lower part was detected by X-ray CT images (Fig. 3). Two other cores with burrows from vegetated surfaces had a more uniform and denser soil matrix. Burrowing led to local compaction only in the loosest bottom parts of the one core. Most remarkably, the CT-scans revealed vesicular pores in the cores from initial surfaces without burrows (as reported from desert soils) and of mm-scale sedimentary layers with a thickness of only a few particles.

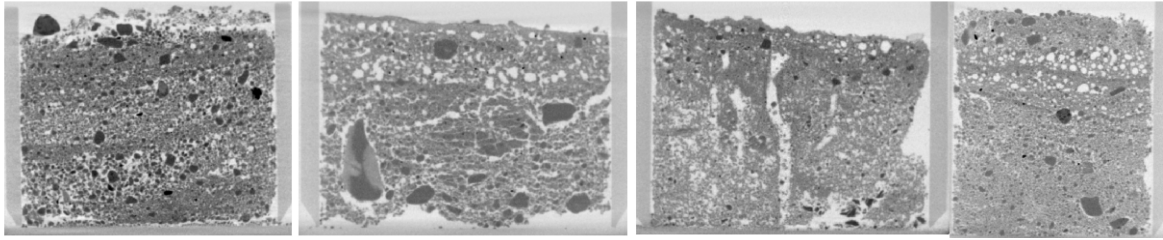


Fig. 3: CT images of 3 cm long surface soil samples (from left to right) catchment east, west, near pond; Experimental Area (the grey scale corresponds with the density, white is pore, and black is mineral particle).

Initial soil surfaces without burrows: The infiltration patterns, visualized with neutron radiography, showed relatively homogeneous proceeding of infiltration fronts for the three slab-type samples. The flow in the ‘west’-sample was affected by a clay clod on the left side, and accumulated water in the uppermost millimeters. The infiltration front of the ‘east’-sample appeared relatively homogeneous and propagates more rapidly and at a relatively constant velocity. The slab from the site near the pond shows isolated water droplets resting on the soil surface, indicating water repellency effects. Despite the apparent water repellency at the surface, wetting fronts remain stable inside the soil. The micro-CT scans revealed characteristic initial structural developments of the uppermost soil surface. One sample (western site) with relatively finer texture had a denser surface seal with few vesicular pores. The other core (eastern site) had several depositional layers formed by sand-size particles that were transported by water. The vesicles were absent in two replicate cores, where the texture was almost pure sand. The ‘lake’-site samples had a structural seal underneath of a new depositional crust similar that looked similar as in the comparable image of the neutron radiographic sample.

Soil surfaces with burrows: The CT-scans revealed micro-morphological and structural modifications that resulted from burrowing activity. The region around the burrow was locally compacted only in a few samples. In both samples infiltration and flow was affected by the channels. For an initially moist sample, the infiltration front remained relatively homogeneous although flow tended more towards higher rates in the burrow. For the initially dry sample, the infiltration front became non-uniform and the burrow acted as preferred flow path (Fig. 4). Previous qualitative water drop penetration time tests on air dry soil below the surface revealed water repellency.

### 2.3 Soil hydraulic measurements

Large variability was found partly because the soil texture ranged from sand (70 locations), weakly clayey sand (93), weakly silty to weakly loamy sand (55), and medium loamy sand (82) to strongly loamy sand (5). Within the catchment, infiltration measurements at 22 locations revealed saturated hydraulic conductivity ( $K_s$ ) values ranging between  $30 \text{ cm d}^{-1}$  and  $800 \text{ cm d}^{-1}$ . Values indicated that a structural crust reduced the hydraulic conductivity.

Outside the fence, four locations were selected for core sampling. The sites were selected based on aerial photos and known soil properties to ensure the comparability with sediment and structures inside the catchment. Also three sites in the catchment were sampled in cooperation with subproject B1.

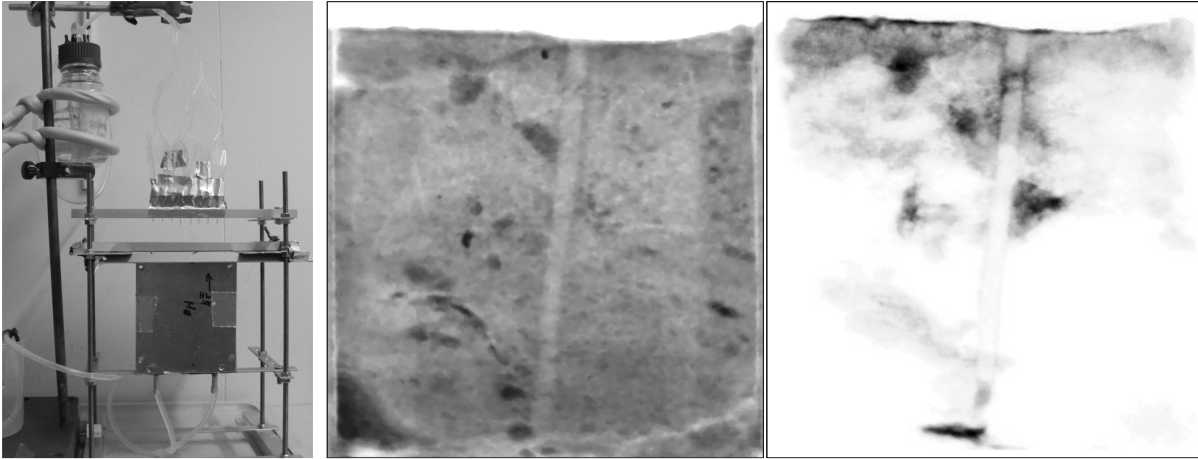


Fig. 4: Experimental device (left) and radiographs of the infiltration experiment with initially air dry soil sample with a central burrow for the H<sub>2</sub>O-free radiographs (centre) and the 2D volumetric water content distributions at about 30 minutes of drip irrigation (right); volumetric water contents range from light grey (> 5 %) to black (< 25 %).

## 2.4 Hydraulic properties inside erosion rills

The hydraulic properties inside erosion rills (stream bed sediments, subproject B5) characterize the local sediment morphology. The field infiltration rates on the rill surface substrate and erosion fan surface substrate at 5 points resulted in  $K_s$ -values of around 200 cm/day. Detailed core sampling of intact rill sediment yielded  $K_s$ -values in a wide range between 100-1,500 cm d<sup>-1</sup> for rel. high bulk densities around 1.85 g cm<sup>-3</sup>; values were mostly higher than in the unsorted original sediment and higher in horizontal than in vertical direction indicating anisotropy caused by this structured layering.

Because of the lower clay content of the surface soil at the Experimental Area as compared to that of the catchment, the crust formation was different; and since the investigation started three years after the construction of the catchment, we missed the very initial situation (“point zero”).

## 3 Comparison to work of others

Similar work regarding a combined irrigation-infiltration-runoff measurement system has hardly been reported elsewhere to our knowledge. The neutron beam experiments visualizing unsaturated steady flow in intact cores are using comparable visualization techniques as experiments that are studying the root water uptake (e.g., Carminati et al., 2009). However, we attempted to use intact soil samples and defined unsaturated flow conditions.



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## **Project B1 – Spatio-temporary development of root growth, decay and exudation in the initial phase of the ecosystem genesis**

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### **1 Introduction**

In phase I of the CRC/Transregio 38, sub-project B1 investigated interactions between the development of plant root systems and the heterogeneity of soil properties during initial ecosystem genesis. The project started out from the general hypothesis that, with the establishment of vegetation during ecosystem genesis, plant roots become key agents in the creation of structures and patterns in soil formation, but that the influence of plants on such pattern formation is driven by mutual interaction, as existing heterogeneities in soil properties in turn shape root growth allocation and activity patterns. Thus, already initially existing heterogeneities resulting from the construction process of the experimental Chicken Creek Catchment may have an important influence on the development of vegetation and soil patterns.

In particular, roots form pathways for water flow and solute transport (directly via soil penetration as well as indirectly by promoting shrinkage through water extraction) and are a primary source of soil organic matter, exuding organic compounds and depositing residues as litter above and below ground (Hütsch et al., 2002). The release of organic compounds, protons and carbon dioxide, consumption of oxygen, uptake of nutrients and water are all processes that lead to steep gradients in chemical conditions and biological activities around roots, a phenomenon well known as “rhizosphere effect” (Hinsinger et al., 2005). These gradients influence patterns of soil weathering, formation of humus and secondary minerals, soil structure and others.

One consequence of root activity and turnover is redistribution of nutrients. This effect is of particular relevance under conditions of low availability of an essential nutrient. When the supply of a growth-limiting nutrient is non-uniform, then plants with the ability to allocate foraging capacities preferentially to patches with increased availability have a competitive advantage in comparison to others that do not have such ability. A common and well-known response of many plant species to patchiness in the distribution of growth-limiting nutrients is root proliferation in nutrient-rich patches (Robinson, 1994). Also physiological adaptations have been reported, but much more rarely, as they are much more difficult to detect than changes in growth rates and morphological parameters (Hodge, 2004).

Limitations in supply of macronutrients such as nitrogen (N) and phosphorus (P) in soils are a frequent condition in the early phases of ecosystem development. While N can be obtained via microbial fixation of atmospheric N, mineral weathering usually is the only relevant source of P at this stage. In fact, an initial survey revealed considerable small-scale heterogeneity in soil properties, including easily soluble P, in the freshly constructed Chicken Creek Catchment (Papritz et al., 2010).

Several plant species have developed specialized root modifications to cope with low P availability in soil. The most prominent modifications are mycorrhizal association and cluster roots. Cluster roots are densely packed groupings of rootlets with determined growth and enhanced organic acid exudation to increase the mobilization of P from soil (Lamont, 2003).

Given this background, the main goal of project B1 in Phase I was to determine the rooting strategies of two plant species that were abundant on the catchment during that phase, the grass *Calamagrostis epigeios* and the legume *Lotus corniculatus*, how they responded to patchiness in soil P, and how, in turn, the roots of these two plant species affected important soil properties, in particular soil pH, nutrient concentrations and the exudation of organic compounds. Additionally, we investigated the effect of heterogeneous water and P distribution on cluster root allocation of *Lupinus albus* - a model plant species for cluster root research.

## 2 Results

*Calamagrostis epigeios* L. Roth and *Lotus corniculatus* L. exhibited different rooting strategies. The root surface density of *L. corniculatus* roots was higher in the topsoil but not in the subsoil than that of *C. epigeios*, while there was no difference in the depth profiles of root length density between the two species. Minirhizotron observations revealed that root growth started much earlier in *L. corniculatus* than in *C. epigeios* during the growing season. Thus, root growth patterns did not only differ in space, but also in time between the two species, suggesting different effects on soil water and nutrient extraction.

The two plant species showed substantially different effects on various chemical and physical properties of the soil. *L. corniculatus* roots decreased the soil pH much more than *C. epigeios* roots. Only after one year, the growth of *L. corniculatus*, *Trifolium arvense* and *C. epigeios* contributed to an increase in soil organic carbon and total nitrogen content. The difference was particularly strong in close vicinity to the roots (“rhizosphere soil”), but also present further away in the “bulk soil” (Boldt et al. 2012).

The homogeneously-appearing initial soils are characterized by finer-textured soil clumps (fragments) of different sizes that are embedded in a sandy matrix. The results suggest that finer-textured fragments embedded in sandy matrix, can have favorable effect on plant and root development during the initial stages of establishment of vegetation cover. The fragments can act as water and nutrient hot spots to improve supply of moisture and essential nutrients for pioneering plants, especially in coarse-textured soil (Boldt-Burisch et al. 2012).

The establishment of *L. corniculatus* and *C. epigeios* on the experimental area after a year resulted in strong decrease of phosphorus, potassium, manganese and zinc in the top 0-20 cm soil depth, and increase in calcium concentrations in bulk soil. This effect increased with increase of vegetation density. Soil nutrient levels after one year of plant establishment were generally lower under *C. epigeios* than under *L. corniculatus* cover.

There were strong differences between the spectrum of organic acids from root exudates in the rhizosphere of *L. corniculatus*, *T. arvense* and *C. epigeios*. The widest range of organic acids was found in the rhizosphere of *L. corniculatus* followed by that of *T. arvense*. For *C. epigeios*, the spectrum was very low (only two organic acids were detected) but the total amount of organic acids was much higher for *C. epigeios* than for the legumes.

Results of germination experiments showed that competition effects between *L. corniculatus*, *T. arvense* and *C. epigeios* occurred during germination. The growth of *L. corniculatus* was positively influenced by the presence of *T. arvense* and *C. epigeios*.

Field plot experiments with in-growth cores as well as container experiments showed a significant influence of patchiness in the spatial distribution of soil phosphate on root allocation by *L. corniculatus*. Roots were preferentially allocated in P fertilized zones.

For *L. corniculatus* growing in undisturbed soil at the Experimental Site and the Chicken Creek Catchment, root uptake had a stronger influence on the correlation between P and root length density than the preferential allocation of roots into P-enriched soil areas. This effect was already detected for one-year-old plants. The depletion of P following root uptake in soil more distant to the root surface suggests that arbuscular mycorrhizal fungi may have played a role in P uptake (Felderer et al., 2013a; Felderer et al., 2013b).

Arbuscular mycorrhizal fungi (AMF) were found to override the patchiness effect on root allocation by *Lotus japonicus* in controlled laboratory experiments in which  $\gamma$ -ray sterilized soil taken from the Experimental Area of the Collaborative Research Center (CRC) was inoculated either with a monospecific culture of the AMF *Glomus intraradices* or with enriched autochthonous AMF (Felderer et al.: Interaction between root growth allocation and mycorrhizal fungi in soil with patchy P distribution. Paper submitted to Plant and Soil). For *L. japonicus* well defined clones are available unlike for *L. corniculatus*.

Thus, it was used as an experimental surrogate of *L. corniculatus* in order to minimize the influence of genetic heterogeneity on root growth. In treatments with patchy application of P and AMF inoculation, root growth was enhanced on the non-fertilized as much as on the fertilized sides of the containers, while there was a significant difference in root allocation between the two sides in absence of AMF. In the absence of AMF and with no P fertilization, root and shoot growth were both strongly inhibited. AMF inoculation without P fertilization enhanced shoot growth as much as P fertilization without AMF inoculation, while root growth was enhanced much less than in the P fertilization treatments. In combination, AMF inoculation and P application enhanced shoot growth even more than each treatment alone, independently of the spatial distribution of the added P fertilizer. There was no dependence of AMF root colonization on the soil P level.

In a climate chamber experiment we demonstrated that locally increased available P concentrations had no effect on cluster root allocation, while heterogeneous water distribution strongly influenced cluster root production within the root system of *L. albus* (Felderer, et al.: Cluster root allocation of *Lupinus albus* in soil with heterogeneous P and water distribution. Paper submitted to Journal of Experimental Botany). In water limited plants, cluster roots were preferentially allocated in the dryer soil with lower available water capacity. By using neutron radiography, we could show that water conductivity was substantially lower in parts of soil with low water availability compared to parts with increased water availability. Consequently, the diffusivity of organic acids released by cluster roots decreased in the dryer soil. Due to this effect, cluster root allocation in soil with lower water content might be beneficial as the organic acid concentration at the cluster root surface could be higher in dry soil compared to moist soil and consequently P-solubilization is improved.

### **3 Conclusions**

In summary, these results support the initial hypothesis of the project and suggest that the two plant species have different effects on the soil water regime and on nutrient cycling. The observation that AMF overrode the effect of P patchiness has not been reported before in the literature and thus appears to be novel. As preferential growth of *L. corniculatus* roots into P-enriched soil cores was also found in the field plot experiment, this raises the question about the importance of autochthonous AMF in the latter. It may explain why no significant difference in shoot growth was found between treatments with P-fertilized soil cores and unfertilized control cores.

Neutron radiography (NR) proved to be a very useful technique to compare treatment effects of uniform and non-uniform water and P applications on root system development without disturbance under laboratory conditions.

The project helped to improve NR imaging and image analysis procedures substantially. Now much better contrasts are achieved, allowing continuous tracing of even very fine roots with the help of software that had been specially developed for this purpose previously at the ETH Chair of Soil Physics.

Apart from being performed in the context of a research program on initial ecosystem genesis, our work is unique by looking simultaneously in both directions of soil-root interactions involved in soil formation and vegetation establishment: soil heterogeneity effects on plant root system development as well as the effects of plant roots on pattern formation in soil chemical properties and soil biological activities. We are not aware of similar work elsewhere.

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## **Project B3 – Influence of different pioneering plants on microbial food web development in soil during initial states of ecosystem development**

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### **1 Introduction**

Compared to climax ecosystems, less complex biological network structures are typical for initial stages of ecosystem development (Schaaf et al., 2011). Pioneer plants in these ecosystems are of central importance, as they drive development of soil properties and food webs mainly through root morphology, rhizodeposition and litter production (Bardgett, et al., 1999; Bardgett & Walker, 2004). However, the exact mechanisms how such pioneer plants influence soil microbial communities and their activity is still not well understood. Quality and quantity of plant litter and exudates often differs from well-studied plant species used in agriculture or forestry.

Differences in rhizodeposition and litter quality of pioneer plants may influence nutrient acquisition by plants, hence promoting plant growth in a nutrient limited environment (Grayston et al., 1998; Wardle et al., 1999). However, due to a reduced supply with nutrients, plants in initial ecosystems may also have a changed resource allocation which subsequently determines the production of secondary metabolites and competitiveness (Müller et al., 2000). This in turn influences litter quality and hence the soil microbial biomass. Whereas root exudates are readily assimilable by single microbes due to the simple structure of these compounds (Baudoïn et al., 2003), the transformation of litter needs complex interactions between microbes, as compounds like lignin or cellulose are difficult to degrade (Dilly et al., 2004; Fioretto et al., 2005). As a consequence, microbial interactions that develop during litter degradation may provide important resources that are highly necessary for ecosystem development (Bardgett & Walker, 2004).

### **2 Results**

#### **2.1 Influence of litter from two pioneer plant species on the formation of microbial food web structures in initial soil ecosystems**

To analyze the influence of litter from two pioneer plant species on the formation of microbial food web structures in initial soil ecosystems a greenhouse experiment was performed in microcosms using <sup>13</sup>C labeled litter material from *Lotus corniculatus* and *Calamagrostis epigejos*, both typical plants for the vegetation found at the Chicken Creek area.

The  $^{13}\text{C}$  labeled litter material has been produced according to Esperschütz et al. (2009) and Gülland et al (2012) using  $^{13}\text{C}$ - labeled  $\text{CO}_2$ . The obtained litter material (*Leucanthemopsis alpina*  $\delta^{13}\text{C} = 88.4 \pm 1.6 \text{‰}$  vs V PDB; *Calamagrostis epigejos*  $\delta^{13}\text{C} = 136.8 \pm 0.6 \text{‰}$  vs V-PDB; *Lotus corniculatus*  $\delta^{13}\text{C} = 101.3 \pm 2.1 \text{‰}$  vs V-PDB) was also used by several other subprojects for litter decomposition experiments (A2, B5, Z1).

For the microcosm study, soil substrate from the Experimental Area near “Chicken Creek” was used. The soil had an average pH of  $5.9 \pm 0.5$  ( $\text{H}_2\text{O}$  1:2.5 w/v). Organic carbon and nitrogen content were determined at  $0.35 \pm 0.03 \%$  and  $0.18 \pm 0.00 \%$ , respectively. The soil was sieved  $< 2 \text{ mm}$  and filled into microcosms (10 cm in height and 14.4 cm in diameter) with a bulk density of  $1.4 \text{ g cm}^{-3}$ . Soil water content was kept at 55 % of the maximum water holding capacity throughout the experiment. The microcosms were incubated at  $10^\circ\text{C}$  in the dark. All treatments were performed in 5 replicates. Five grams of oven dried plant litter were mixed into the first centimeter of the soil in the microcosm. The detritosphere was harvested 4, 12 and 40 weeks after litter addition to the soil. For quantification of litter degradation rates, in addition microcosms with litterbags were installed. Additionally, microcosms where no litter had been added have been used as controls and were sampled at each sampling time point. We postulated that (1) these two colonizer plants provide litter of different quality, hence resulting in different rates of litter decomposition. Therefore (2) different structures and dynamics of microbial degraders’ food webs are established in the detritosphere.

Plant litter of both, *Lotus* and *Calamagrostis* decreased significantly during the experimental period of 40 weeks. Although only four harvesting time points were used, a statistical significance of  $p < 0.0001$  was detected with an  $R^2 = 0.9813$  for *Calamagrostis* litter decomposition and  $R^2 = 0.9965$  for *Lotus* T treatments, respectively. After 40 weeks of litter incubation, non degradable litter residues of 36.2 % ( $\pm 1.7$ ) and 25.4 % ( $\pm 2.4$ ) of the initial amounts of *Calamagrostis* and *Lotus* litter, respectively, were found.

Our data revealed high contents of  $C_{\text{mic}}$  ( $275.74 \pm 7.37 \text{ mg kg}^{-1} \text{ DW}$ ) in combination with a highly enriched  $^{13}\text{C}$  signature in  $C_{\text{mic}}$  ( $+89.72 \pm 2.75 \text{‰}$   $\delta^{13}\text{C}$  vs V-PDB) in the microcosms with *Lotus* litter supporting the hypothesis of a fast incorporation of plant litter C into the microbial biomass during the initial phase of litter degradation. As *Lotus* plant litter was higher in nitrogen content and of low C/N ratios, microbial degraders were obviously positively stimulated in this treatment. High ratios of C/N in *Calamagrostis* plant litter probably resulted in limited litter degradation and consequently lower contents of  $C_{\text{mic}}$  (approx.  $70 - 105 \text{ mg kg}^{-1} \text{ DW}$ ). Furthermore *Calamagrostis* litter was higher in stem fractions and hence lignin and cutin contents, which additionally influenced microbial degradation.

Delta  $^{13}\text{C}$  signatures in  $C_{\text{mic}}$  showed a constant decomposition of *Calamagrostis* plant litter during the experimental period, probably due to a slow but continuous nutrient release. Lower  $^{13}\text{C}$  signatures in *Calamagrostis* compared to *Lotus* may additionally be explained by a priming effect of the microbial biomass towards utilization of older soil organic matter.

Based on the total PLFA pattern obtained from the different microcosms (mol %), the influence of the applied litter type as well as the sampling time point on the microbial community structure during the experimental period was evident (Fig. 1).

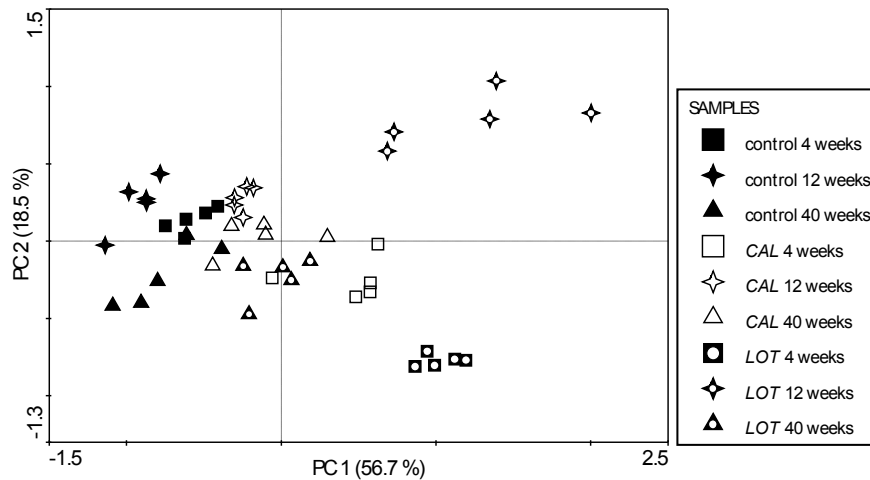


Fig. 1: Principal components analysis (PCA) of the PLFA dataset (content of 28 individual PLFA on the basis of mol %). The ordination plot shows the first two principal components (PC; scaling focused on interspecies correlations). The percentage of variance explained by the ordination axes is given in parentheses. Symbols illustrate samplings after 4, 12, and 40 weeks of the microcosm experiment for the control treatment (control), *Calamagrostis epigejos* (CAL), and *Lotus corniculatus* (LOT), respectively ( $n = 5$ ). Individual points represent the microbial community structure associated with discrete microcosms. PCA was done with the Canoco 4.5 software package (Microcomputer Power, Ithaca, USA) using the covariance matrix.

Fig. 2 illustrates the abundances of different PLFA subgroups in the two treatments at different time points of sampling, as well as the distribution of carbon derived from the applied amount of (labelled) plant litter, calculated according to Elfstrand et al. (2008) and Moore-Kucera & Dick (2008). Four weeks after litter application, ant-sat, mon-unsat and pol-unsat PLFA subgroups showed highest abundance in samples from both litter types (Fig. 2a, b). According to Zelles (1999), ant-sat PLFA have been used as indicators for Gram positive bacteria, whereas mon-unsat and pol-unsat represent Gram-negative bacteria and micro-eukaryotes (fungi and protozoa). This was confirmed by  $^{13}\text{C}$  PLFA analyses (Fig. 2c, d), where highest percentages of the labeled plant litter C were detected in Gram-positive and Gram-negative bacteria as well as micro-eukaryotes (roughly 30 %, 35 % and 20 % respectively).

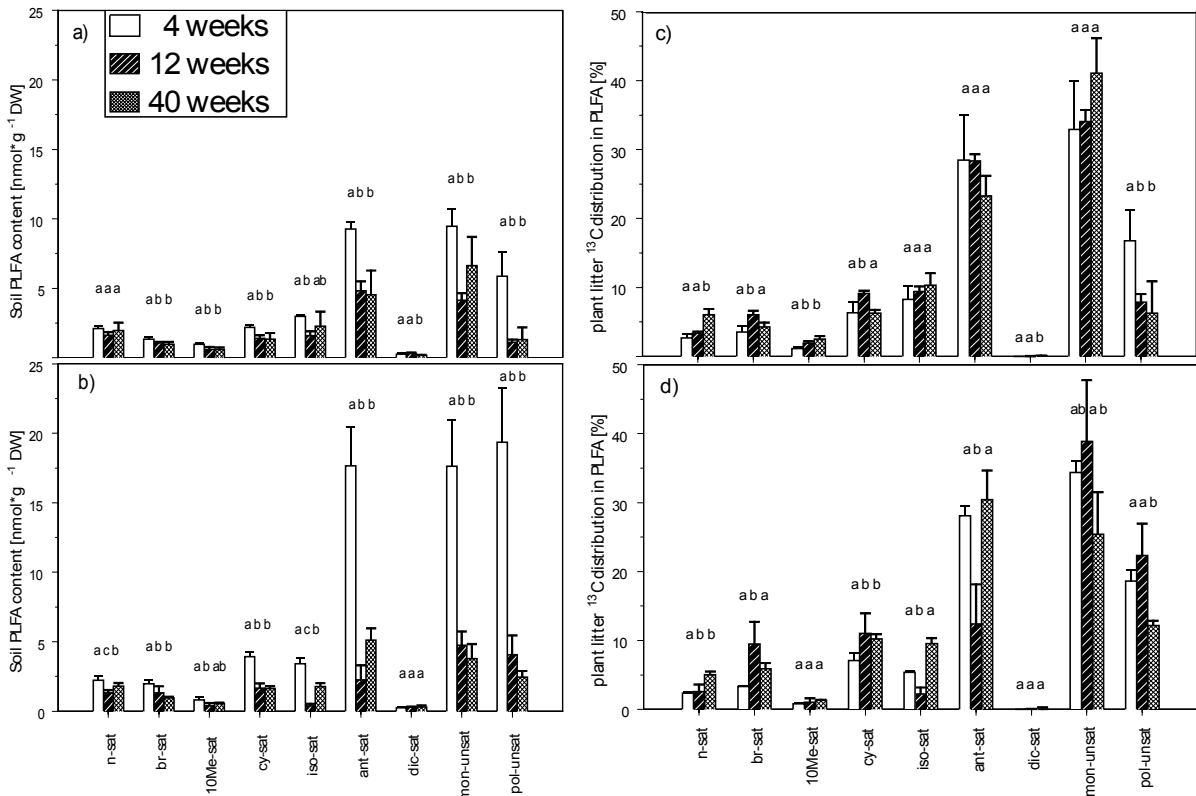


Fig. 2: PLFA contents [ $\text{nmol g}^{-1} \text{DW}$ ] of PLFA sub-groups +) in soil at 4, 12 and 40 weeks after application of *Calamagrostis epigejos* (a) and *Lotus corniculatus* (b) plant litter. Distribution of plant litter  $^{13}\text{C}$  in PLFA sub-groups [%] was shown in (c) for *Calamagrostis epigejos* and (d) for *Lotus corniculatus* plant litter (means  $\pm$  standard deviation,  $n = 5$ ). For each sub-group, a oneway ANOVA followed by Tukey-HSD post-hoc-tests was performed; differences between harvesting timepoints  $p < 0.05$  are represented by different characters.

After 12 weeks of litter incubation, microbial biomass has decreased significantly ( $p < 0.05$ ) as indicated by almost every individual PLFA subgroup (Fig. 2a, b). Especially those groups that dominated the microbial community after 4 weeks of degradation showed a rapid decline. This may be explained by a decrease of opportunistic  $r$  strategists that have been highly involved in the decomposition of plant litter at the beginning of the degradation process (Atlas & Bartha, 1998; Dilly, et al., 2004). After 12 weeks of litter incubation, pol-unsat PLFA indicated that fungal and protozoan abundance (Fig. 3b) as well as their litter degrading activity (Fig. 3c) was still higher in *Lotus* treatments compared to *Calamagrostis* (Fig. 3a, c).

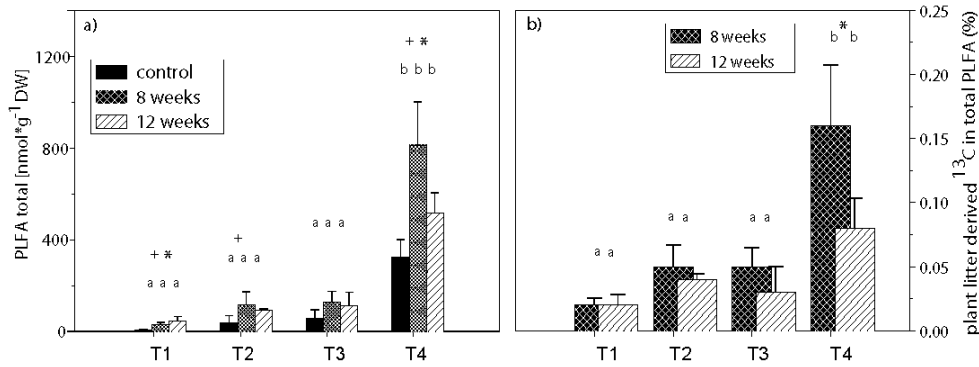


Fig. 3: Total PLFA content (a) in soil ( $\text{nmol g}^{-1} \text{DW}$ ) and litter derived  $^{13}\text{C}$  incorporation (b) into total PLFA at different stages of ecosystem development T1-T4 and individual harvesting time points. Illustration based on means  $\pm$  stdev,  $n = 5$ . Letters (a, b) represent significant differences  $p < 0.05$  between stages of ecosystem development within one treatment. Asterisks (\*) indicate differences between litter incubation time points whereas +) represents statistically significant differences  $p < 0.05$  between litter and control treatments (taken from Esperschütz et al. 2011a).

40 weeks after application of the litter material, the microbial turn-over and a rapid microbial die-off resulted in a release of (labeled) C compounds into the soil.  $^{13}\text{C}$  derived from plant litter was detected in all PLFA fractions, hence also organisms that are not directly involved with the litter decomposition process may benefit from the plant C that was originally provided by the litter material.

In summary, (1) different litter quality of the two coloniser plants *Lotus* and *Calamagrostis* result in different rates of litter degradation. Due to the individual litter composition and nutrient extent released into the soil matrix, (2) a diverse structure of microbial degrader food webs has been established. Obviously not only the quality of the carbonous material is important for the structure of microbial litter degraders but also the amount of available nitrogen, which is limited in the initial substrate material. Consequently different pioneer plants promote microbial food web development and ensure soil quality and hence productivity in initial ecosystems. According to the results from the present study, a highly dynamic and adaptive microbial community structure has been induced by *Lotus* litter application, whereas a stable microbial community structure has been promoted by *Calamagrostis* litter. However in both treatments, plant litter C could already be detected in all microbial PLFA sub-groups 4 weeks after litter incubation started. This indicates a fast transformation of plant litter derived C into the microbial food web and highlights the importance of biotic interactions within the soil microbial community, which ensure growth and nutrient supply of the community members (Esperschütz et al., 2011b).

## 2.2 Microbial food web dynamics along a chronosequence of a glacier forefield

Experiments along the forefield of the Dammaglacier were performed to generalize the data obtained from the microcosm experiment. Therefore in a litter degradation experiment, carbon fluxes from plant litter into soil and soil microbial communities were measured along the forefield of the Damma glacier (Switzerland).  $^{13}\text{C}$  enriched litter of the pioneering plant *Leucanthemopsis alpina* L. (obtained as described above) was applied at sites that have been free of ice for approximately 10 years (T1), 60 years (T2) and 100 years (T3); furthermore a site outside the forefield (> 700 years of ecosystem development) was used as reference (T4). After snow melt 2008 in the beginning of June, tubes made of aluminium (20 cm in diameter and 14 cm in height) were installed 10 cm deep into the soil with five replicates at every location (T1-T4). Eight weeks and 12 weeks after litter application, litter bags and soil were harvested. It was hypothesized (1) that microbial abundance and diversity increases with progressing ecosystem development. These results in (2) a higher plant litter decomposition rate and a progressive specialization of the microbial community structure with increasing ecosystem development. According to Bardgett & Walker (2004), it is further assumed that (3) the microbial community of soil becomes increasingly dominated by fungi as primary succession proceeds.

After 12 weeks of litter incubation, plant litter degradation was almost similar at all sites, except the initial site near the glacier end (T1), where significant higher amounts of plant litter were not degraded. The total soil PLFA content ( $\text{nmol g}^{-1}$  DW) increased with proceeding ecosystem development (Fig. 3a). Litter application resulted independent from the site in an increase of the PLFA content compared to the control samples at all sampling time points.  $^{13}\text{C}$  incorporation into total PLFA was correlated to ecosystem development, with higher values at the well-developed sites T3 and T4 (Fig 3b).

According to the total PLFA content, the soil microbial biomass was low at the initial site T1, comparably to the substrate at the research site “Chicken Creek”. After the glacier retreat, predominantly sand and rocks were present at the newly exposed terrain. A highly patchy vegetation structure was able to establish during the first years after ecosystem development, depending on water availability and substrate quality. Although sites were chosen for the experiment, where vegetation (especially *Leucanthemopsis alpina*) was already rudimentary present, soil development was still at the beginning, low in structure and nutrients and hence microbial colonization. At T2 and T3, representing around 60 years and approximately 100 years of ecosystem development, the microbial biomass was higher compared to T1. An increasing microbial abundance was observed with ecosystem development and nutrient availability. At the chosen reference site T4, where the age of ecosystem development was supposed to be at least more than 700 years, a high soil microbial biomass indicates a highly advanced stage of ecosystem development.

As a measure of microbial diversity, the Shannon Diversity index was calculated on the basis of total PLFA concentrations and the number of fatty acids detected in the samples (Tab. 1). In control treatments without litter addition, Shannon Diversity increases with ecosystem development. The index ranges from 2.3 to 2.9, except in the control treatment at the 10-year-old site T1, where a Shannon index of only 1.6 was calculated. Similar indices and trends were detected after 8 weeks and 12 weeks of litter application, whereas the lowest index was always observed at T1. The Shannon Evenness, indicating the similarity of the frequencies, was lowest (0.67 - 0.69) at the young site T1 in control as well as in both litter treatments. An increase could be observed with ecosystem development in all treatments.

A lower microbial diversity was suggested at the young 10-year-old site T1 compared to the more developed sites. Due to the limited availability of nutrients, especially C and N, near the glacier end, only microbes that are specialized towards the specific nutrient sources may have been present in higher contents. This was supported by the Shannon Evenness, indicating a higher microbial variation and higher dominance of certain microbes at the younger sites. An increasing variety of nutrient sources at more developed sites, results in a highly diverse microbial community structure. Consequently litter application caused a stimulative effect on the microbial diversity mainly at T1.

The ratio of fungi - bacteria decreased with proceeding site development. Higher ratios were detected due to litter application, except at the 10-year-old site. Fungi therefore obviously were one of the dominant microbial groups at the young site near the glacier. However this is contradictive to previous studies, where the microbial community of soil becomes increasingly dominated by fungi as primary succession proceeds (Bardgett & Walker, 2004). This may be explained at least partly by the fact that fungi were expressed as sum of PLFA 18:1 $\omega$ 9 and 18:2 $\omega$ 6,9. According to literature, these PLFA did not exclusively characterize fungi (Pombo et al., 2002; Zaady et al., 2010). At the 10-year-old research site T1, high ratios as well as high abundances of PLFA 18:1 $\omega$ 9 and 18:2 $\omega$ 6,9 may also indicate high occurrence of cyanobacteria, since these lipids also commonly found in this microbial group.

According to Reichhardt et al. (1997) and Ratledge & Wilkinson (1989), the ratio of MUFA precursors to cyclopropyl PLFA was calculated on the basis of the sum of  $\omega$ 7 MUFA (16:1 $\omega$ 7 and 18:1 $\omega$ 7) to its cyclopropyl derivatives, cy17:0 and cy19:0 as a stress indicator. At all sites T1 – T4, an increasing ratio was detected due to litter application, whereas with proceeding site development a decrease could be observed (Tab. 2). A decreasing ratio with increasing ecosystem development suggests a higher microbial stress at well-developed sites. The authors suggest this as a phenomenon of microbial stress due to and increasing nutrient competition at sites with higher microbial diversity. At sites of low microbial diversity, a high specialization of microbes with respect to the nutrient sources prevents microbial competition. Litter application increased the ratio at all sites, but no changes were observed within the total trend. Since nutrients at the Experimental Areas have been low, due to the additional amount

Tab. 1: Overview about microbial diversity and evenness (Shannon indices), microbial stress ( $\sum \omega^7 / \sum cy$ ) and distribution of fungi / bacteria at all stages of ecosystem development 8 weeks and 12 weeks after litter application, as well as without litter. Values were illustrated as means of five replicates  $\pm$  standard deviation. Letters (a, b, c) indicate significant differences  $p < 0.05$  between different stages of ecosystem development.

	Control										8 weeks			12 weeks				
	10		60		100		> 700 y		10	60	100	> 700 <		10	60	100	> 700 y	
<b>Shannon Diversity</b>	1.600 (0.154) a	2.733 (0.111) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b	2.869 (0.082) b
<b>Shannon Evenness</b>	0.667 (0.004) a	0.839 (0.034) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b	0.861 (0.025) b
$\sum \omega^7 / \sum cy$	1.656 (0.045) a	1.504 (0.237) a	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab	1.305 (0.245) ab
<b>fungi / bacteria</b>	1.290 (0.866) a	0.057 (0.023) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b	0.057 (0.029) b



of litter derived nutrients, better conditions for microbial growth have been adapted at all sites. However, the nutrient competition among the given microbial diversity (stated above) at individual sites remained unaffected.

In summary, the total PLFA content, indicative for the soil microbial biomass in soil, increased with proceeding ecosystem development. According to the Shannon Diversity, this is accompanied by a higher microbial diversity. Hence results from the Damma forefield showed (1) an increasing microbial abundance and diversity with proceeding ecosystem development. The PLFA stress indicator fatty acids in addition evidenced the higher microbial diversity and abundance was attended by an increased physiological stress, suggested due to nutrient competition.

However plant litter decomposition was almost similar at all investigated sites at the end of the relatively short vegetation period of 12 weeks. Therefore litter decomposition was not influenced by ecosystem development, microbial biomass content and microbial diversity in soil (2). Contradictive to recent findings, higher proportions of fungi were detected at less developed sites (3). However, in this study the fungal biomarker needs further consideration, since similar lipids were synthesized by cyanobacteria, which are commonly detected at the sites near the Damma glacier end (Esperschütz et al., 2011a; Esperschütz et al., 2012).

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## **Project B4 – Formation and importance of functional redundancy for microbial nitrogen transformation during initial states of ecosystem development**

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### **1 Introduction**

Initial ecosystems are characterized by low nutrient content and scarce vegetation (Sigler & Zeyer, 2002; Tscherko et al., 2003). Consequently, the amount of available carbon (C) and nitrogen (N) is low during initial ecosystem development. In contrast bacterial richness is high during initial soil formation (Sigler & Zeyer, 2002). This observation is in agreement with studies reporting highest diversity of functional groups, such as nitrate reducers and N fixing microbes (Duc et al., 2009; Deiglmayr et al., 2006; Schmalenberger et al., 2009). Moreover, initial sites are often dominated by microbes belonging to the r-strategists being able to respond quickly to changing environmental conditions, while with continuing succession a shift to k-strategists occurs that rather pursue the strategy of maintenance (Sigler & Zeyer, 2002). In contrast to these studies, some reports found no significant correlation between soil age and diversity or increasing diversity (Tscherko et al., 2003; Nemergut et al., 2007).

Glacier forefields offer an excellent opportunity to study the alterations of nutrient cycles as well as single turnover processes during soil development. Therefore in the last decades different studies at glacier forefields focused on the dynamic of selected processes and transformation steps of the N cycle (Deiglmayr et al., 2006; Duc et al., 2009; Kandeler et al., 2006) because N as a macronutrient is essential for ecosystem development, but most bedrocks do not contain any N. Many authors have postulated the importance of N fixation at initial stages of soil development (Kohls et al., 1994; Schmidt et al., 2008). However, there are conflicting data on the role of mineralization. Tscherko et al. (2003) reported a distinct acceleration of N mineralization after 50 years of soil development, in parallel with the buildup of organic matter. This observation is in agreement with the assumption that autotrophic communities consisting of cyanobacteria, algae, lichens and mosses play a major role in early ecosystem development (Walker & del Moral, 2003; Schmidt et al., 2008). These organisms are often tightly associated and form structures known as biological crusts.

Biological crusts are followed by heterotrophic organisms. However, Bardgett et al. (2007) found evidence for a significant mineralization activity also at the initial phases of soil development which was related to the degradation of ancient and recalcitrant soil organic matter. Similarly, the development of denitrification over time remained vague. On the one hand, high gene abundance (copies per ng DNA) of *nirS* (nitrite reductase) and *narG* (nitrate reductase) were observed in pioneer soils (Kandeler et al., 2006) on the other hand, the nitrate reductase activity peaked in developed soils (Deiglmayr et al., 2006). Recent data on the development of nutrient cycles based on chronosequence studies on glacier forefields has been summarized in a recent review (Schulz et al., 2013a).

## **2 Results**

The key issue of CRC/Transregio 38 was to study the processes in early ecosystem development at Chicken Creek and to reveal the basic ecological concepts. However, in order to reveal general concepts and to come up with ecological models with a high predictive power it has been essential not only to focus on a single ecosystem but also to work with a number of reference systems characterized by different bed rock features and climatic conditions. It was decided to use dunes and glacier forefields as reference systems.

### **2.1 Methodological developments**

#### **2.1.1 Improved nucleic acid extraction**

In the frame of the project an improved protocol, allowing the simultaneous extraction of DNA and RNA from soil using phenol-chloroform with subsequent column-based separation of DNA and RNA (PCS) was developed (Töwe et al., 2011). This new approach was compared with the well-established protocol published by Griffith et al. (2000), where DNA and RNA are separated by selective enzymatic digestions and two commercial kits used for DNA or RNA extraction, respectively, using four different agricultural soils. Yield and purity of the nucleic acids as well as abundance and diversity profiles of the soil bacterial communities targeting the *nosZ* gene via quantitative real-time PCR and terminal restriction fragment length polymorphism on DNA and RNA level were compared.

The newly developed protocol provided purer nucleic acid extracts compared to the used kit-based protocols. All protocols were suitable for DNA- and RNA-based gene quantification, however high variations between replicates were obtained for RNA samples using the original Griffiths protocol. Diversity patterns of *nosZ* were highly influenced by the extraction protocol used both on the DNA and RNA level. Finally, the data showed that the new protocol allows a simultaneous and reproducible extraction and separation of DNA and RNA, which were suitable for reliable analyses of gene and transcript copy numbers and diversity pattern.

### **2.1.2 Improvement of real time PCR**

Real-time quantitative PCR (qPCR) is a widely used technique in microbial community analysis, allowing the quantification of the number of target genes in a community sample. In the frame of this project the standard-curve (SC) method which is widely employed for the absolute quantification has been improved. As the SC method assumes that the amplification efficiency (E) is the same for both the standard and the sample target template. We analyzed 19 bacterial strains and nine environmental samples in qPCR assays, targeting the *nifH* and 16S rRNA genes. The E values of the qPCRs differed significantly, depending on the template. This has major implications for the quantification. If the sample and standard differ in their E values, quantification errors of up to orders of magnitude are possible. To address this problem, we propose and test the one-point calibration (OPC) method for absolute quantification. The OPC method corrects for differences in E and was derived from the  $\Delta\Delta C(T)$  method with correction for E, which is commonly used for relative quantification in gene expression studies. The SC and OPC methods were compared by quantifying artificial template mixtures from *Geobacter sulfurreducens* (DSM 12127) and *Nostoc commune* (Culture Collection of Algae and Protozoa [CCAP] 1453/33), which differ in their E values. While the SC method deviated from the expected *nifH* gene copy number by 3- to 5-fold, the OPC method quantified the template mixtures with high accuracy. Moreover, analyzing environmental samples, we show that even small differences in E between the standard and the sample can cause significant differences between the copy numbers calculated by the SC and the OPC methods (Brankatschk et al., 2012).

Furthermore high and comparable efficiency values are the key for reliable quantification of target genes from environmental samples using real-time PCR. Therefore it was the aim of another study to investigate if PCR amplification efficiencies of plasmid DNA used for the calculation of standard curves (i) remain constant along a logarithmic scale of dilutions and (ii) if these values are comparable to those of DNA extracted from environmental samples. It could be shown that comparable efficiency values within the standards cannot be achieved using log scale serial dilutions and a comparison of gene copy numbers from DNA extracted from environmental samples and standard DNA extracted from plasmids is only possible in a very small interval (Töwe et al., 2010a).

## **2.2 Microbial community structure and function during ecosystem development**

### **2.2.1 The ecology of nitrogen turnover during ecosystem development: Functional microbial communities and their activities along a chronosequence of a glacier forefield**

Glacier forefields offer an excellent opportunity to study the alterations of nutrient cycles as well as single turnover processes during soil development. In this study we examined the ecology of the microbial nitrogen (N) cycle in bulk soil samples from a chronosequence of the Damma glacier, Switzerland.

Major processes of the N cycle were reconstructed on the genetic as well as the potential enzyme activity level at sites of the chronosequence that have been ice-free for 10, 50, 70, 120 and 2000 years (a), respectively. In our study, we focused on N fixation, mineralization (chitinolysis and proteolysis), nitrification and denitrification (Brankatschk, et al., 2011).

Quantifications of the C and N pools revealed that soil nutrient status changed substantially along the glacier forefield. From 10 a to 2000 a the C and N pools increased by an order of magnitude.  $C_{mic}$  increased from 58 to 902  $\mu\text{g C g}^{-1}$  and the values correlated with the amount of extractable DNA ( $n = 25$ ,  $R^2 = 0.53$ ,  $p < 0.001$ ). Similarly, total organic C (TOC) increased from 0.7 to 40  $\text{mg C g}^{-1}$ . On the other hand,  $C_{mic}$  correlated poorly with cell counts and the abundance of *rpoB* gene copy numbers ( $n = 25$ ,  $R^2 = 0.31$ ,  $p = 0.004$  and  $n = 25$ ,  $R^2 = 0.11$ ,  $p = 0.099$ ; respectively). The C/N ratios were in the range of 12 to 15 and relatively constant. In young soils (e.g. 10 a) the nitrate concentrations were much higher than the ammonium concentrations. However, the ammonium concentrations steadily increased along the glacier forefield. In mature soils (e.g. 2000 a) the ammonium concentrations were one order of magnitude higher than the nitrate concentrations.

Potential enzyme activity was related to soil dry weight as well as the amount of extracted DNA to obtain a biomass-independent parameter (Fig. 1). Generally, potential enzyme activities related to dry soil increased along the chronosequence. N fixation activity was below the detection limit in samples 10 a to 70 a (detection limit 0.2  $\text{pmol N h}^{-1} \text{g}^{-1}$ ), but ranged between 1 and 3  $\text{pmol N h}^{-1} \text{g}^{-1}$  in samples 120 a and 2000 a. Relative N fixation activity was similar in samples 120 a and 2000 a. As proxy for potential mineralization activity (relative to  $\mu\text{g}$  of DNA), protease and chitinase assays were performed. Significant increases of protease activity from 5 to 25  $\text{nmol MUF h}^{-1} \text{g}^{-1}$  as well as of chitinase activity from 14 to 72  $\text{nmol MUF h}^{-1} \text{g}^{-1}$  were observed along the chronosequence. At the same time, relative mineralization activity tended to decrease. Potential nitrification activity increased significantly from 0.1 (10 a) to 2.3  $\text{nmol NO}_2^- \text{-N h}^{-1} \text{g}^{-1}$  (2000 a). The same pattern was observed for potential denitrification activity, where activities increased from 1.8 to 40  $\text{nmol N}_2\text{O-N h}^{-1} \text{g}^{-1}$ . The relative nitrification and denitrification activities resulted in similar pattern but did not reach significant levels in most cases.

Gene copy numbers were related to g soil as well as ng DNA (Fig. 2). Abundance of *nifH* gene was lowest in sample 10 a ( $2 \times 10^6$  copies  $\text{g}^{-1}$  soil) and increased up to  $2 \times 10^7$  copies  $\text{g}^{-1}$  soil in soil samples from 50 a. In the soil samples from sites that have been ice-free for longer period *nifH* gene abundance decreased. Similar results were obtained when data were related to ng extracted DNA. Abundance of genes coding for enzymes involved in mineralization significantly increased (Fig. 3): *aprA* genes from  $6 \times 10^6$  to  $4 \times 10^7$ ; *chiA* genes from  $7 \times 10^5$  to  $9 \times 10^6$  copies  $\text{g}^{-1}$  soil. In contrast, relative abundances (related to ng of DNA) of both genes involved in mineralization were constant (Fig. 3b) at all sites.



Abundance of the nitrification marker gene *amoA* was studied for ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB). While *amoA* AOB gene abundances showed no significant differences related to g of soil, AOA significantly increased from  $3 \times 10^4$  to  $8 \times 10^5$  copies  $g^{-1}$  soil. Generally, AOB abundances were 80-times higher compared to AOA at the 10 a, 50 a and 70 a site, whereas the AOB to AOA ratios were close to 2 in soil samples from the 120 a and 2000 a site. Relative *amoA* AOA gene abundances remained stable,

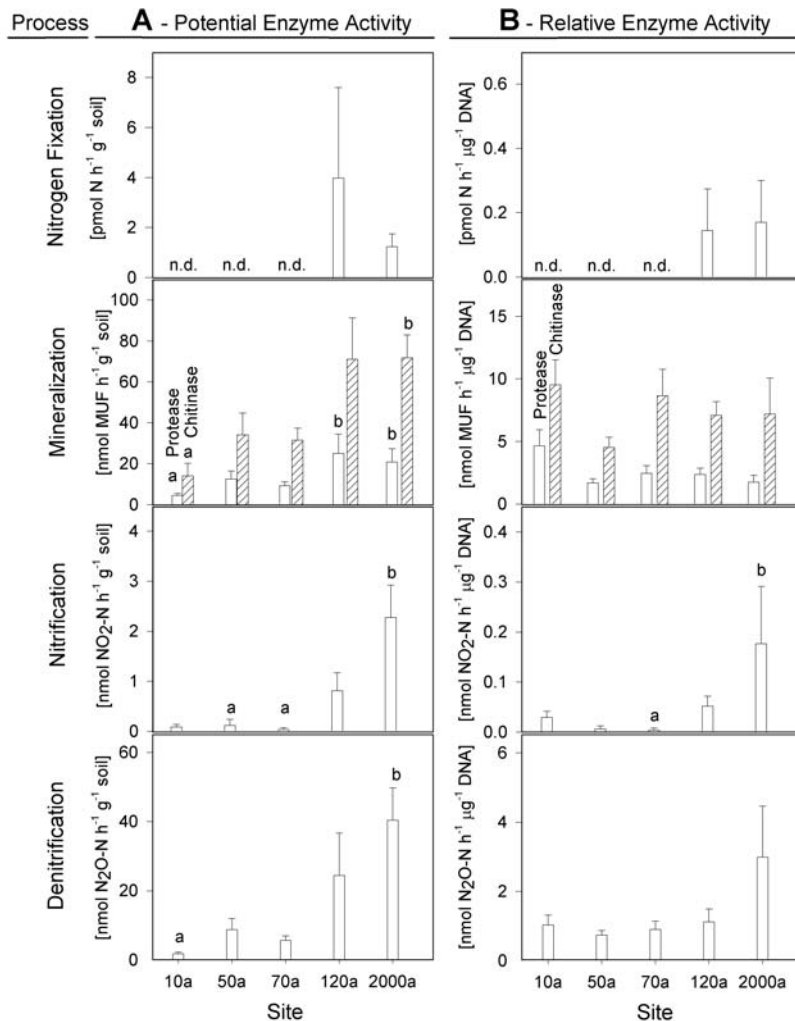


Fig. 1: Potential (A) and relative enzyme activities (B) for nitrogen fixation, mineralization, nitrification and denitrification are displayed (n = 5, error bars represent standard error of means). Only significant differences as revealed by one way ANOVA on ranks (p < 0.05) are indicated by different letters. n. d. indicates that all five replicates of potential N fixation were below the detection limit of 0.2 pmol N h<sup>-1</sup> g<sup>-1</sup> soil (taken from Brankatschk et al., 2011, ISME J, 5, 1025-1037).

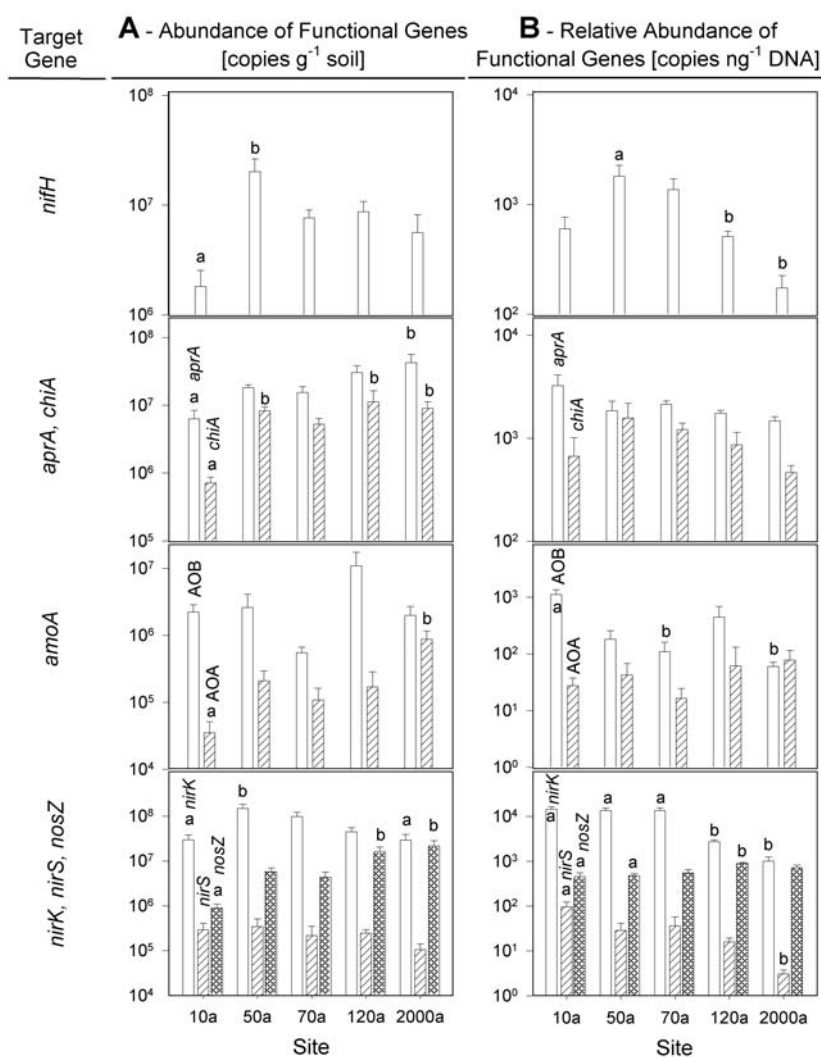


Fig. 2: Gene copy numbers of functional genes involved in major steps of the nitrogen cycle (*nifH*, *aprA*, *chiA*, *amoA* AOB, *amoA* AOA, *nirK*, *nirS* and *nosZ*) are displayed related to g<sup>-1</sup> soil (A) and ng<sup>-1</sup> DNA (B) (n = 5, error bars represent standard error of means). Only significant differences as revealed by one way ANOVA on ranks (p < 0.05) are indicated by different letters (taken from Brankatschk et al., 2011, ISME J, 5, 1025-1037).

whereas relative *amoA* AOB gene abundances significantly decreased from  $1.4 \times 10^3$  to  $7.2 \times 10^2$  copies ng<sup>-1</sup> DNA along the chronosequence. To quantify the denitrifying bacteria, genes coding for the nitrite reductases (*nirK*, *nirS*) and nitrous oxide reductase (*nosZ*) were measured. Generally, *nirK* gene abundances were two orders of magnitude higher than *nirS*. Gene abundances of *nirK* decreased from  $1.5 \times 10^8$  to  $3 \times 10^7$  copies g<sup>-1</sup> soil along the chronosequence. *NosZ* gene copy numbers were lowest in sample 10 a with  $9 \times 10^5$  copies g<sup>-1</sup> soil but equaled *nirK* gene abundance at site 2000 a. Relative gene abundances showed comparable patterns for denitrification genes except *nirS*, which decreased along the chronosequence.

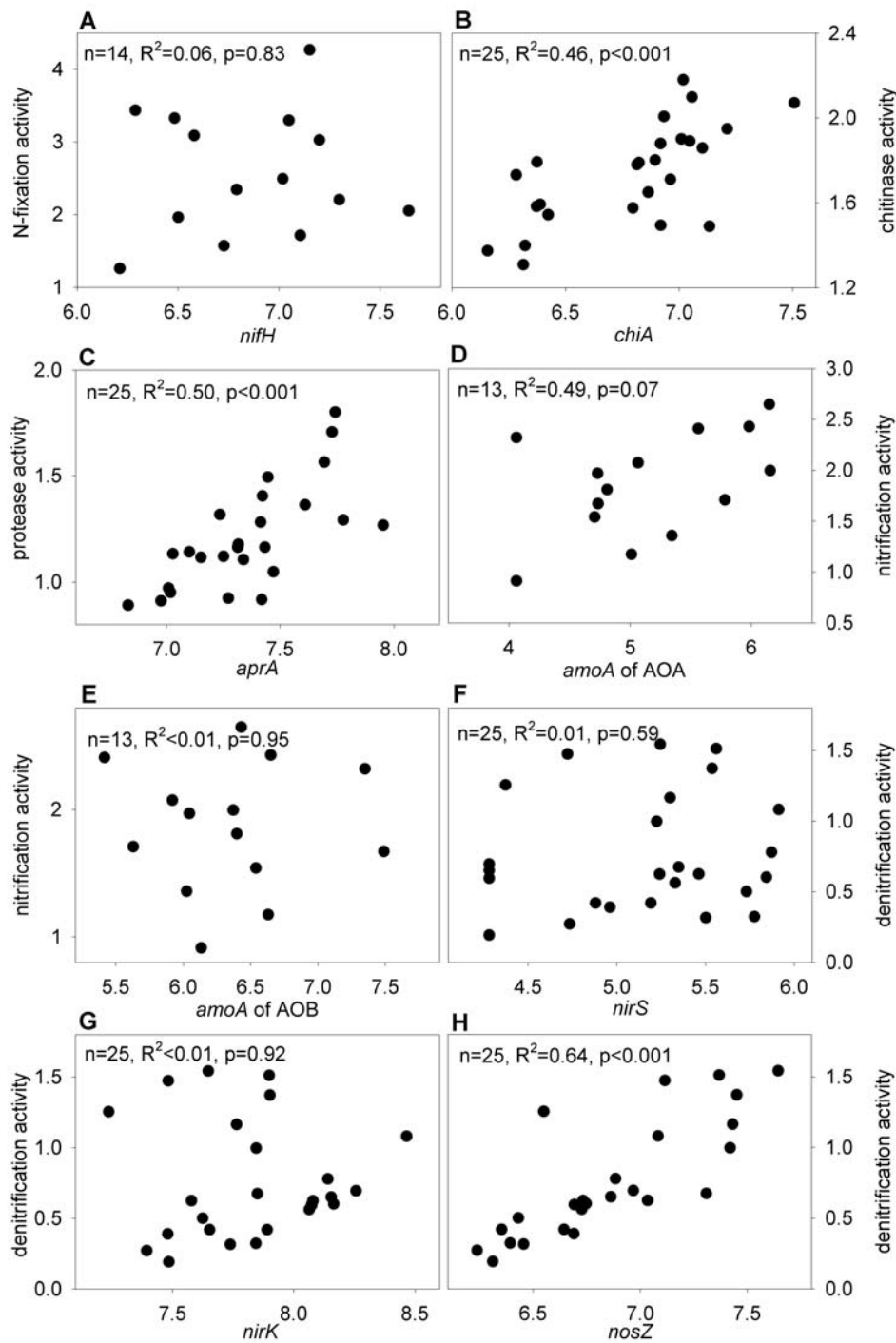


Fig. 3: Correlations of the gene copy numbers and the corresponding potential enzyme activities are displayed for nitrogen fixation (A), mineralization (B, C), nitrification (D, E) and denitrification (F, G and H). The graphs plot log-transformed copy numbers vs. log-transformed enzyme activities. In the top left corner of each plot the parameters of the regression analysis, including p-values of t-tests, are provided (taken from Brankatschk et al., 2011, ISME J, 5, 1025-1037).

Correlations between gene abundance pattern (copies g<sup>-1</sup> soil) and potential enzyme activities (g<sup>-1</sup> soil) were assessed. In order to reduce variability and to include all available data points, both data sets were log-transformed prior to regression analysis (Fig. 3). While *nifH*, *amoA* AOB, *nirS* and *nirK* gene abundances did not correlate with the corresponding potential enzyme activities, significant correlations with the potential enzymatic activities were found for *chiA*, *aprA*, *amoA* AOA and *nosZ* gene copy numbers significantly correlated with the potential enzyme activities ( $\alpha = 0.1$ ).

In summary, our results suggest that mineralization, mainly the transformation of deposited organic material, was the main driver for N turnover in initial soils i.e. ice-free for 10 a. Transient soils being ice-free for 50 a and 70 a were characterized by high levels of nitrogen fixation. In developed soils, ice-free for 120 a and 2000 a, significant rates of nitrification and denitrification were measured. Surprisingly, copy numbers of the respective functional genes encoding the corresponding enzymes were already high in the initial phase of soil development. This clearly confirms that not the genetic potential is the driver for certain functional traits in the initial phase of soil formation but rather a well-balanced expression of the respective genes coding for selected functions.

### 2.2.2 Succession of N cycling processes in biological soil crusts on a Central European inland dune

Biological soil crusts (BSCs) are microbial assemblages that occur worldwide and facilitate ecosystem development by nitrogen (N) and carbon accumulation. N turnover within BSC ecosystems has been intensively studied in the past; however, shifts in the N cycle during BSC development have not been previously investigated. Our aim was to characterize N cycle development first by the abundance of the corresponding functional genes and second by potential enzyme activities; we focused on the four processes: N fixation (*nifH*), mineralisation as proteolysis and chitinolysis (*chiA*), nitrification (*amoA*) and denitrification (*nosZ*). We sampled from four phases of BSC development and from a reference located in the rooting zone of *Corynephorus canescens*, on an inland dune in Germany. BSC development was associated with increasing amounts of chlorophyll, organic carbon and N. Potential activities increased and were highest in developed BSCs. Similarly, the abundance of functional genes increased. We propose and discuss three stages of N process succession. First, the heterotrophic stage (mobile sand without BSCs) is dominated by mineralisation activity. Second, during the transition stage (initial BSCs), N accumulates, and potential nitrification and denitrification activity increases. Third, the developed stage (established BSCs and reference) is characterised by the dominance of nitrification (Brankatschk et al., 2013).

### 2.2.3 Abundance of microbes involved in nitrogen transformation in the rhizosphere of *Leucanthemopsis alpina* (L.) HEYWOOD grown in different soils from a chronosequence of glacier forefield

In this study, we reconstructed major parts of the nitrogen cycle in the rhizosphere soil/root system of *Leucanthemopsis alpina* (L.) HEYWOOD as well as the corresponding bulk soil by quantifying functional genes of nitrogen fixation (*nifH*), nitrogen mineralization (*chiA aprA*), nitrification (*amoA* AOB, *amoA* AOA) and denitrification (*nirS*, *nirK*, and *nosZ*) in a 10-year (10 a) and a 120-year (120 a) soil and linked to the carbon and nitrogen status of the soil and the plant. The experiment was performed in a greenhouse using the climatic conditions of the glacier forefield. Samples were taken after 7 and 13 weeks of incubation (Töwe et al., 2010b).

Mean values of plant carbon and nitrogen contents were calculated. While the carbon content did not differ between both sampling time points and both treatments, the nitrogen content significantly increased in the plants cultivated in the 10a soil from 1.28 (T1) to 3.94% (T2). Contrary, it was stable in the plants of the 120 a soil. Consequently, the C/N ratio dropped in the 10 a samples to 10.3, whereas it remained at a constant average level of 22 in the plants grown in the 120 a soil. Absolute values of carbon and plant biomass revealed a 2-fold increase of the plants from T1 to T2 planted in the 10 a soil and a 9-fold increase of the plants cultivated in the 120 a soil. Total nitrogen content increased 4-fold and 5-fold in the plants from the 10 a and the 120 a soil, respectively.

Values for ammonium were very low or even below the detection limit ( $< 0.04 \text{ mg NH}_4^+\text{-N kg}^{-1}$ ) for all BS and RRC samples from the 10 a soil. In contrast, a time dependent decrease of the ammonium concentration was observed in the BS and RRC samples of the 120 a soil. Nitrate concentrations also differed between the two soils but were further significantly influenced by the soil compartment. Thus values were much higher in the RRC than in the BS, peaking in  $49.33 \text{ mg kg}^{-1}$  (RRC, T1) in the 10 a soil and  $108.26 \text{ mg kg}^{-1}$  (RRC, T1) in the 120 a soil, respectively.

All functional genes investigated were highly influenced by the soil compartment. Higher gene copy numbers were determined in the RRC compared to BS samples (Fig. 4). Interestingly, highest *nifH* gene copy numbers were detected in RRC samples of the 10 a soil with  $1.7 \times 10^7$  copies  $\text{g}^{-1}$  dw after 7 weeks of incubation. As *nifH* gene abundance was significantly influenced by incubation time in the 10 a soil ( $p = 0.008$ ), gene abundance was strongly reduced in RRC after 13 weeks to a level of  $8 \times 10^6$  copies  $\text{g}^{-1}$  dw. A similar trend for a time dependent decrease of *nifH* gene copy numbers was also observed in the bulk soil samples from the 10a soil. In contrast, *nifH* gene abundance was neither influenced by incubation time nor by soil compartment in the 120 a soil. Gene abundance of *chiA* was significantly higher in samples of the 120 a soil compared to those of the 10 a soils. In the 10 a samples a strong RRC effect ( $p = 0.0$ ) was visible at both sampling time points with six times higher *chiA* abundances in RRC compared to BS.

However, no time dependent changes were observed in the 10 a soil. In the 120 a soil a significant interaction of the factors soil compartment and incubation period was revealed ( $p = 0.021$ ), which is uncovered by rather similar gene abundances ( $1 \times 10^8$  copies  $g^{-1}$  dw) in the BS and RRC at T1 and dispersing gene abundances at T2. *AprA* gene copy numbers were below the detection limit in all cases ( $< 10^4$  *aprA* gene copies  $g^{-1}$  dw).

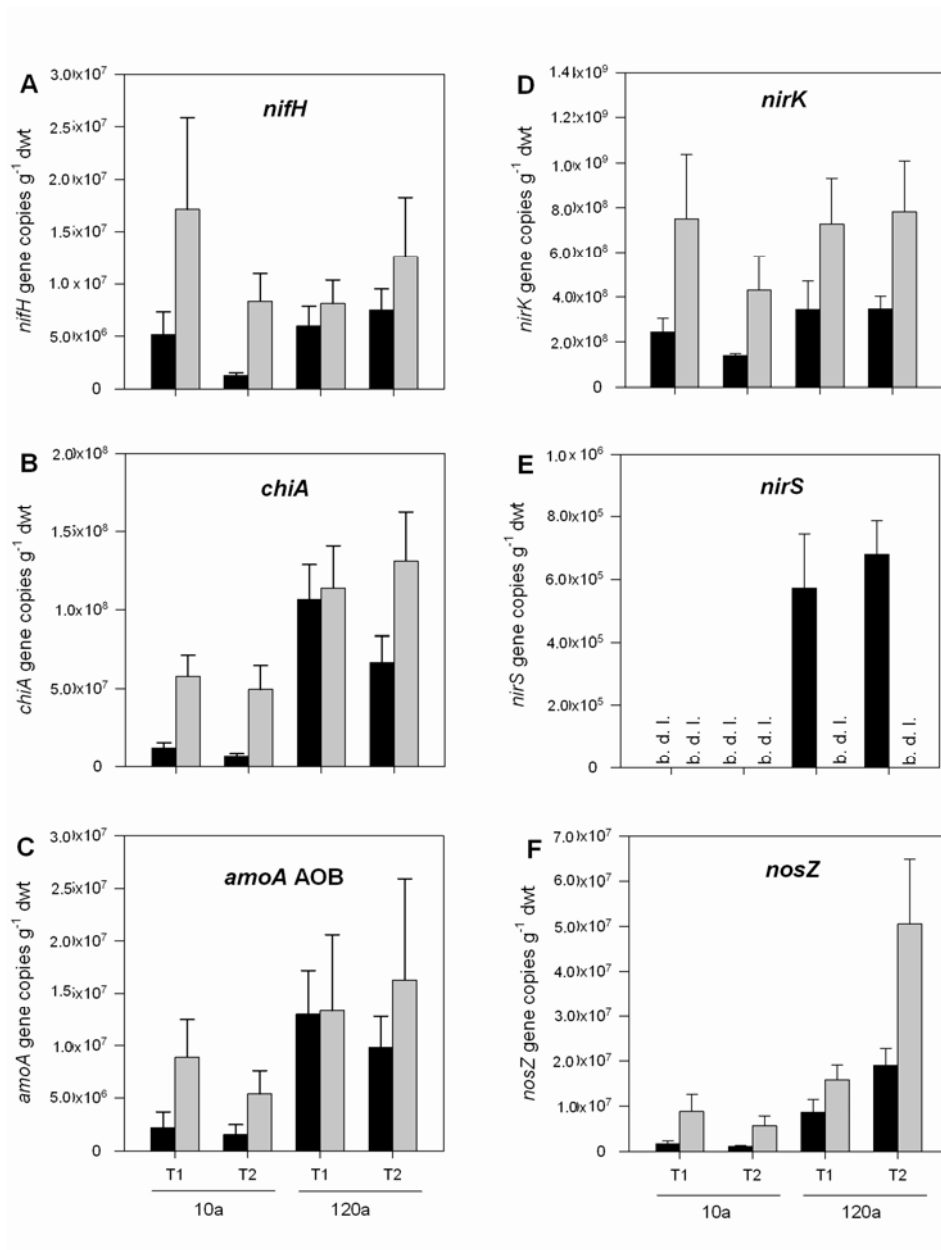


Fig. 4 Copy numbers of functional genes involved in the nitrogen cycle (*nirK*, *nirS*, *nosZ*, *nifH*, *chiA* and *amoA* AOB) are displayed for RRC [light colored bars] samples of *L. alpina* and the corresponding BS [black colored bars] after 7 (T1) and 13 weeks (T2) of incubation in a 10 a and 120 a soil ( $n = 5$ , error bars represent standard deviations). "b.d.l." indicates that samples were below detection limit of  $10^4$  gene copies  $g^{-1}$  dw (taken from Töwe et al., 2010b)

Independent of sampling time point and soil compartment ammonium-oxidizing bacteria (AOB) clearly dominated in numbers over ammonium-oxidizing archaea (AOA), which were in all cases below the detection limit ( $10^4$  *amoA* gene copies  $g^{-1}$  dw soil; data not shown). While a strong RRC effect ( $p = 0.0$ ) on *amoA* (AOB) gene abundance was detected in the 10 a soil, it was negligible in the 120 a soil. Accordingly, up to five times higher values were measured in RRC of the 10 a soil, peaking in  $8.9 \times 10^6$  copies  $g^{-1}$  dw after 7 weeks of incubation, compared to the bulk soil. Contrary, rhizosphere and bulk soil samples of the 120 a soil showed no significant differences and revealed an average gene abundance of  $1.3 \times 10^7$  *amoA* (AOB) copies  $g^{-1}$  dw. While *nirK* gene copy numbers ranged between  $1.1 \times 10^8$  (10 a, BS, T2) and  $7.8 \times 10^8$   $g^{-1}$  dw (120 a, RRC, T2), *nirS* genes were only observed in the bulk soil of the 120a soil ( $5.7$  (T1) and  $6.8 \times 10^5$  copies  $g^{-1}$  dw (T2)). The abundance of the *nirK* gene was strongly impacted by the soil compartment ( $p = 0.0$ ) in both soils. Additionally, incubation time had a significant ( $p = 0.011$ ) influence in the 10 a soil, resulting in a decrease of gene abundance from 7 to 13 weeks of in RRC and BS as well. In contrast to *nirK*, *nosZ* gene copies remained constant over time in the 10 a soil with average gene abundances of  $1.4$  and  $7.2 \times 10^6$  copies  $g^{-1}$  dw in BS and RRC, respectively. In the 120 a soil the *nosZ* gene abundance was significantly influenced by incubation time ( $p = 0.0$ ) and soil compartment ( $p = 0.0$ ). Thus the *nosZ* gene copy numbers significantly increased in RRC of the 120 a soil, peaking in  $5.1 \times 10^7$  copies  $g^{-1}$  dw after 13 weeks of incubation. This is in contrast to all other genes measured, which were more influenced by the soil compartment than incubation time in the 120 a soil.

In summary, highest *nifH* gene abundance in connection with lowest nitrogen content of *L. alpina* was observed in the 10a soil after 7 weeks of incubation. These results demonstrate the important role of associative nitrogen fixation for plant development at these sites. In contrast in the 120 a soil copy numbers of genes involved in denitrification, mainly *nosZ*, were increased after 13 weeks of incubation, indicating an overall increased microbial activity status as well as higher concentrations of nitrate in the soil

#### **2.2.4 Diversity pattern of nitrogen fixing microbes in nodules of *Trifolium arvense* (L.) at different initial stages of ecosystem development**

Legumes can be considered as pioneer plants during ecosystem development, as they form a symbiosis with different nitrogen fixing *Rhizobia* species, which enables the plants to grow on soils with low available nitrogen content. In this study we compared the abundance and diversity of nitrogen fixing microbes based on the functional marker gene *nifH*, which codes for a subunit of the nitrogenase gene, in nodules of different size classes of *Trifolium arvense* (L.). Additionally, carbon and nitrogen contents of the bulk soil and plant material were measured. Plants were harvested from different sites, reflecting 3 (3 a) and 5 (5 a) years of ecosystem development, of an opencast lignite mining area in the south of Cottbus, Lower

Lusatia (Germany) where an artificial catchment “Chicken Creek” was constructed to study the development of ecosystems. Plants from the 5 a site revealed higher amounts of carbon and nitrogen, although *nifH* gene abundances in the nodules and carbon and nitrogen contents between the two soils did not differ significantly. Analysis of the *nifH* clone libraries showed a significant effect of the nodule size on the community composition of nitrogen fixing microbes. Medium sized nodules (2-5 mm) contained a uniform community composed of *Rhizobium leguminosarum* bv. *trifolii*, whereas the small nodules (< 2 mm) consisted of a diverse community including clones with non-*Rhizobium nifH* gene sequences. Regarding the impact of the soil age on the community composition a clear distinction between the small and the medium nodules can be made. While clone libraries from the medium nodules were pretty similar at both soil ages, soil age had a significant effect on the community compositions of the small nodules, where the proportion of *R. leguminosarum* bv. *trifolii* increased with soil age (Schulz et al., 2013b).

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## **Project B5 – C transformations during initial stream succession**

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### **1 Introduction**

Streams in recently formed landscapes have been proposed to undergo three successive stages distinguished largely by changes in vegetation structure of the stream corridor (Grimm, 1994, Mutz et al., 2002, Milner & Gloyne-Phillips, 2005). An initially barren open-land stage is followed by a stage characterized by macrophytes in the stream channel and by forbs and graminoids in the riparian zone until shrub and tree growth leads to the establishment of woodland. Instream metabolism is initially dominated by benthic primary production that fuels heterotrophic biofilm communities (Romaní & Sabater, 1999), complemented by ancient organic matter that is mobilized from the substrate in the catchment (Hood et al., 2009). Later, when forbs and graminoids encroach, the plants provide increasing amounts of terrestrial litter to stream communities while sunlight still reaches the stream bed and enables algal growth. Eventually, however, in the woodland stage, riparian shrubs and trees will form a closed canopy that limits light penetration and algal development (Sabater et al., 2000) while delivering large amounts of litter as a resource for stream communities (Benfield, 1997). This successional trajectory thus entails marked shifts in the quantities and quality of plant litter supplied to streams.

In addition to successional shifts in the resource base of stream ecosystems, physical structures in stream corridors tend also to change during succession (Milner & Gloyne-Phillips, 2005) and can have consequences for microbial communities and organic matter dynamics. In particular, the hydrological regime in an initially barren catchment is dominated by surface runoff, resulting in frequent peak flows that cause scour and fill of the stream bed and are likely to affect benthic biofilms and stream metabolism. The extent of water exchange between hyporheic and surface stream also influences stream metabolism (Fischer, 2003), because it is afforded to a considerable extent by hyporheic biofilms (Fischer & Pusch, 2001, Battin et al., 2003). Furthermore, benthic biofilms, macrophytes, and wood are important structural elements in streams affecting surface flow patterns and thus also the hydrologic exchange between hyporheic and surface water.

Patches of benthic algal mats can partly clog stream sediments (Grimm, 1994, Battin & Sengschmidt, 1999), whereas macrophytes and wood deposits are hydraulically active structures that increase flow variability and drive vertical water exchange across the stream bed surface (Sand-Jensen, 1998, Mutz et al., 2007). The significance of such structural features for stream metabolism is still poorly understood.

The objective of the observational and experimental investigations presented here was to elucidate how changes in the supply of organic matter and the physical and associated biological structures anticipated by the three-stage succession model affect C transformations during stream ecosystem succession. The studies focused mainly on C transformations in the open-land stage, but two experiments in flumes also addressed the transition to the macrophyte-dominated and woodland stage. Here we summarize the main findings of these investigations. Details of the results have been reported in a series of publications summarized in Tab. 1.

## **2 Stream network formation in the Chicken Creek Catchment**

An extensive stream network, which included permanently flowing stretches, developed unexpectedly fast after construction of the Chicken Creek Catchment in 2005, and enabled us to observe the early stages of stream succession directly in the field. General trends emerging during the first 5 years followed the three-stage model presented above. Gully erosion carved the stream network into the plain surface largely during the barren open-land stage before 2007. Repeated measurements of stream bed levels made in 2009 and 2011 in three streams showed that erosion in the gullies had ceased. Although sediment was still transported during rain events and peak flow in later stages, material originated mainly from lateral erosion of the initially steep, often almost vertical gully banks, which became increasingly regraded. As a result, the stream corridors generally widened during the subsequent macrophyte-dominated stage, with scour still frequently disturbing and sorting the sediments. Wide land-water transition zones developed in upstream ephemeral stretches of the stream network. However, since 2007, developmental trajectories of the three main networks have significantly diverged, probably as a result of differences in sub-catchment size and hence stream power and sediment load. The larger streams were episodically set back to the open-land stage, due to pronounced scour that deeply incised the stream channels and prevented macrophyte colonization, whereas streams draining smaller sub-catchments were bound to be transformed to the macrophyte stage. The smallest ephemeral channels in the network developed towards terrestrial rills lacking regular sediment disturbance, probably because surface runoff and sediment yield was limited from the catchment whose surface was increasingly stabilized by biological crusts (Project A3, p. 25, this issue) and vegetation cover (Project C3, p. 97, this issue). However, higher moisture content in the rills compared to surrounding terrestrial areas facilitated dense growth of grass vegetation, initiating organic-rich terrestrial soils.

Tab. 1: Research topics covered by observational and experimental investigations into C transformations during initial stream succession in the Chicken Creek Catchment.

<b>Research topic</b>	<b>Successional stage addressed</b>	<b>Type of study</b>	<b>Reference</b>
Properties and bioavailability of DOC across a hydrological gradient from soil solution to ground, subsurface and pond water; significance of microbes for DOC utilization	Open-land stage	Field study and experiment	Risse-Buhl et al. (2013a)
Seasonal variability of heterotrophic metabolism across a hydrological gradient from terrestrial soils to ephemeral and perennial streams; significance of water permanence	Open-land stage	Field study	Gerull et al. (2011)
Seasonal variability of heterotrophic microbial community structure and potential enzyme activities across a hydrological gradient from terrestrial soils to ephemeral and perennial streams; significance of water permanence	Open-land stage	Field study	Frossard et al. (2012a)
Significance of shallow and deep sediment disturbance for whole-stream net primary production and community respiration	Open-land stage	Flume experiment	Gerull et al. (2012)
Significance of periodic sediment turnover for ciliate communities in migrating sand ripples	Open-land stage	Microcosm experiment	Risse-Buhl et al. (2013b)
Interactions among hyporheic exchange flow, sediment-associated microbial activity, and sediment disturbance	Open-land stage	Flume experiment	Mendoza-Lera & Mutz (2013)
Responses of microbial enzyme production and community structure on decomposing leaves to shifts in litter quality and quantity during simulated riparian succession	Open-land to woodland stage	Flume experiment	Frossard et al. (2013a)
Responses of microbial productivity on decomposing leaves to shifts in litter quality and quantity during simulated riparian succession	Open-land to woodland stage	Flume experiment	Gerull et al. ( <i>unpublished manuscript</i> )
Litter supply as driver of change in microbial community structure and activity in stream sediments during simulated riparian succession	Open-land to woodland stage	Flume experiment	Frossard et al. (2013b)
Fungal role in C transformations in streams beyond litter decomposition, effects on litter- and sediment-associated microbial communities and whole-stream metabolism	Early woodland stage	Flume experiment	Frossard et al. (2012b)

### **3 Field studies**

#### **3.1 Dissolved organic carbon dynamics**

In the open-land stage, dissolved organic carbon (DOC) in soil solution, upwelling ground water, subsurface water in an alluvial fan, and pond water from the Chicken Creek Catchment all had high DOC concentrations (averages of 6.0-11.6 mg DOC L<sup>-1</sup>; Risse-Buhl et al., 2013a). The <sup>14</sup>C age of groundwater DOC varied between 2600 and 2800 years, suggesting that DOC was partly mobilized from charred organic matter of the Quaternary substrate. In a 70-day incubation experiment, 20 % of the total DOC was found to be bioavailable, irrespective of the origin of the water in the catchment. Origin of microbial communities (enriched from soil, stream sediment or pond water) had only marginal effects on overall DOC utilization. These results indicate that DOC derived from Quaternary substrate can support microbial activity during early ecosystem succession to some extent, although the largest fraction is recalcitrant DOC and appears to be exported from newly formed catchments once it has been mobilized.

#### **3.2 Microbial activities and community structure**

Deposition of vascular plant fragments in stream sediments was associated with increased respiration and created significant heterogeneity in sediment respiration rate within the stream channels (Gerull et al., 2011). Contrary to expectations, both respiration rate and potential enzyme activities of wetted soil and sediment from ephemeral stream sites were similarly high as rates measured with sediments from perennial stream sections (Gerull et al., 2011; Frossard et al., 2012a). This suggests that long-term water availability was not a main factor determining metabolic potential in the early successional stages of the Chicken Creek Catchment.

Potential activities of 10 carbon-, nitrogen- and phosphorus-acquiring enzymes varied little among sites in the catchment, despite contrasting environmental conditions (Frossard et al., 2012a). However, the potential activities showed pronounced seasonal changes, with different patterns for different enzymes tested. There were no or only weak correlations between potential enzyme activities and either water-chemical parameters or sediment and soil organic matter content. Furthermore, the seasonal enzyme patterns were unrelated to changes in the structure of bacterial communities in soil and sediment, reflecting a general lack of either spatial or temporal patterns in bacterial community structure. Carbon turnover in the perennial stream sections was 4 - 8 fold higher than in the ephemeral sections and terrestrial sites (Gerull et al., 2011). However, this difference was insufficient for perennial channels to act as genuine metabolic hot spots. Extrapolated to a full year and the whole catchment, streams contributed only 5 % to total carbon turnover, 95 % being due to terrestrial soils during and after rainfall events. These findings suggest that hot moments are more important for C transformation in early successional landscapes than hot spots.

## 4 Flume and microcosm experiments

A total of 16 experimental flumes (4 m length, 12 cm width, 12 cm depth) were set up immediately adjacent to the Chicken Creek Catchment. They were filled with sediment, fed with ground water from the catchment, and operated in either circulation or partial flow-through mode. We conducted a total of five experiments, which focused on the effects of various factor combinations reflecting different stages of initial stream ecosystem succession on stream metabolism and microbial communities. A range of standard response variables were determined in addition to net community respiration, net community production and hyporheic exchange rate.

### 4.1 Effects of sediment disturbance on stream metabolism during early ecosystem succession

Frequent disturbance of sandy bed sediments is a major characteristic of streams in the initial open-land stage, but effects resulting from different depths of sediment disturbance on whole-system metabolism are poorly known. We assessed such effects by manually disturbing sandy sediments in flumes (to 1 or 4 cm depth) at two occasions. Neither shallow nor deep sediment disturbance affected net community production at the first occasion after 11 days, whereas both disturbance intensities reduced net community production after the second disturbance event after 31 days (Gerull et al., 2012). Net community respiration was unaffected by the first sediment disturbance, whereas the second disturbance caused higher rates following deep compared to shallow sediment disturbance. Initially, when  $P/R < 1$ , the ratio of whole-ecosystem production to respiration ( $P/R$ ) was unaffected. However, the second deep, though not shallow, disturbance when  $P/R$  was  $> 1$  temporarily reset  $P/R$  to  $< 1$ . These results indicate that effects of sediment disturbance on stream metabolism depend on the stage of microbial biofilm colonization. Both shallow and deep disturbances curb algal production while only deep disturbance appears to stimulate heterotrophic activity.

Sediment particles continuously glide, roll or bounce when stream sediments are scoured during periods of high flow. In addition, however, sediments move as migrating sand ripples during base flow, when particles also periodically glide and roll (Baas, 1999). We assessed the effects of continuous and periodical sediment movement on the colonization of ciliates in a microcosm experiment. The frequency of sediment shifting affected the abundance of all three ciliate species studied. A vagile grazer feeder, *Chilodonella uncinata*, and a sessile filter feeder, *Vorticella convallaria*, reached maximum abundances in periodically shifting sediments and also showed positive population growth when sediments moved continuously, whereas *D. campylum* increased in abundance only in stable sediments (Risse-Buhl et al., 2013b). This result suggests that both the vagile grazer feeder (*C. uncinata*) and the sessile filter feeder (*V. convallaria*) could cope with periodically shifting sediments of sandy ripples, outlasting short periods of sediment movement during floods, whereas *D. campylum* could not.

A corollary is that the spatio-temporal pattern of sediment movement acts as critical structuring factor of ciliate communities. Since grazing ciliates affect the structure and activity of microbial biofilms (Risse-Buhl et al., 2012), the findings are likely to have implications for C transformations by biofilms in stream sediments.

#### **4.2 Effects of microbial biofilms and sediment disturbance on hyporheic water exchange and microbial activity in sand-bed flumes**

Algal and bacterial biofilms in sediments of early-successional open-land streams have been hypothesized to affect vertical water flux across sandy sediment surfaces, with potential implications for C transformations in streams (Battin & Sengschmitt, 1999). To gain insights into the relative significance of algae and heterotrophic microorganisms for the dynamics of vertical water flux and stream microbial communities, half of the 16 outdoor flumes in the Chicken Creek Catchment were operated under constantly dark conditions, whereas the eight other flumes were exposed to daylight. Vertical water flux was affected by structures resulting from metabolic processes in the uppermost sediment layer after 13 days (Mendoza-Lera & Mutz, 2013). Algal and bacterial cells embedded in the extracellular polymer matrix of the biofilm and microbially mediated precipitation of  $\text{CaCO}_3$  blocked the sediment pore space and thereby disrupted vertical water flux under both daylight and dark conditions. The blockage was exacerbated under daylight conditions by the production of oxygen bubbles within the uppermost sediment layer. A shallow mechanical disturbance of the sediment applied after 21 days restored the vertical water flux, but respiration and organic matter content remained unaffected. Thus, vertical water flux can be controlled by microbial biofilms and shallow sediment disturbance, producing a patchy and dynamic distribution of vertical water exchange in sand-bed streams.

#### **4.3 Effects of size-sorted sediment particles on hyporheic metabolism**

Hydrological exchange and habitat available for microbial colonization are major factors promoting hyporheic metabolism. However, since sediment particle size affects these two factors in opposite ways, the influence of grain size on hyporheic stream metabolism is not currently clear. We filled 12 of the flumes in the Chicken Creek Catchment with sand (0.2 - 0.8 mm), gravel (2 – 8 mm) or a sand-gravel mixture (25 – 75 % mass) and ran them for 6 weeks before transferring the flume sediments to flow-through columns and percolating them with identical solutes for two additional weeks. A fluorescent tracer was used to measure repeatedly advective solute supply to hyporheic biofilms, which proved constant in the flumes over time and to be twice as high in gravel as in sand or the sand-gravel mixture. Gravel-filled flumes had higher hyporheic respiration rates per particle surface area and showed a trend towards higher potential enzyme activities. In columns, by contrast, no differences in respiration rate or potential enzyme activities were observed among sediment



types. These results suggest that advective solute supply, which increases with larger sediment grains becoming increasingly sorted during early succession in sand-bed streams, is a major factor determining hyporheic metabolism.

#### **4.4 Effects of plant litter quality and quantity on microbial communities and C transformations**

To assess the effects of two types of leaf litter inputs on microbial communities and C transformations we simulated an important aspect of the successional transition of streams from the initial open-land stage dominated by biofilms to the macrophyte-dominated and woodland stage. Our hypotheses were (i) that rates of C transformations and microbial activities in streams increase markedly when streams begin to receive large amounts of leaf litter during stream succession, and (ii) that the structure and activity of microbial communities establishing at different stages of succession depends on the quality of the dominant litter source. We added various types and amounts of litter to the experimental flumes to simulate a key aspect of successional changes when riparian vegetation establishes: 1) no litter addition, 2) grass litter, 3) mix of grass and tree litter, 4) tree litter only, 5) 2.5 times the amount of tree litter. A few leaves of *Calamagrostis epigejos* (wood small-reed or bushgrass, a grass species expected to become dominant in the catchment in the macrophyte stage), *Betula pendula* (silver birch, a species expected to become dominant in the woodland stage) and *Cornus sanguinea* (common dogwood, an easily degradable model species) were exposed in all flumes to determine effects of litter availability on litter decomposition and associated microbial communities. Samples of these leaves were collected and analyzed after 6, 8 and 10 weeks.

Leaf toughness of *Cornus* leaves after 10 weeks in flumes containing tree litter was notably reduced, suggesting faster decomposition in these conditions (Gerull et al., *unpublished manuscript*). The abundance and diversity of fungal spores (aquatic hyphomycetes; Bärlocher 1992, Krauss et al. 2011) did not change among the five simulated successional stages. Microbial activities on tougher birch and grass litter were unaffected by either the quantity or type of litter supplied to the experimental streams (i.e. changing litter standing stock during succession) but differed between the two litter types (Frossard et al., 2013a). This was in stark contrast with bacterial and fungal community structure, which markedly differed not only between birch and grass litter but, to a lesser extent, also among streams receiving different litter inputs. These patterns reveal distinct responses of microbial community structure and activity to the bulk litter available in streams but consistent responses to the litter type colonized.

In sediments, mean potential activities of nitrogen- and phosphorus-acquiring enzymes were 12 - 70 times greater than those of carbon-acquiring enzymes, with the former reduced 1.3 - 8.3 fold in flumes that received tree litter (Frossard et al., 2013b).

These patterns could suggest a gradually diminishing nutrient limitation of microbial activity during riparian succession, potentially linked to an increasing supply by the added litter and to a lower nutrient demand as algal biomass and labile carbon supply by photosynthetic exudates declined. Given that the observed shifts in nutrient-acquiring enzymes were reflected in changes of sediment microbial communities, these results indicate that both the type and density of terrestrial vegetation affect microbial community structure and function in stream sediments, particularly enzyme production related to nutrient cycling.

#### **4.5 Importance of fungi for C transformations and microbial communities in early successional streams**

What is the importance of fungal litter decomposers for stream microorganisms other than fungi and what are the indirect effects on C transformations resulting from such microbial interactions? We addressed these questions in a flume experiment simulating an early woodland stage, characterized by low inputs of birch litter, corresponding to about 250 times lower amounts than those typically received per year by mature forest streams (Benfield, 1997). We hypothesized that the presence of fungi would enhance overall microbial activity, accompanied by shifts in the microbial communities associated with both leaf litter and sediments. Flumes were inoculated with microbial communities that either comprised fungi or with communities from which fungi had been mostly removed by filtration. Ground water was subsequently circulated through the flumes for 5 weeks. We measured whole-ecosystem metabolism and analyzed sediment and leaf litter at five occasions during that time. Net community production, net community respiration and microbial respiration associated with leaf litter were higher when channels were inoculated with fungi (Frossard et al., 2012b). Bacterial biomass on sediment and leaf litter did not vary among treatments, nor did microbial respiration in sediment, except at the last sampling date when respiration greatly increased in the flumes inoculated with fungi. Similarly, an increase in net primary production after three weeks was strongest in the flumes inoculated with fungi, resulting in higher chlorophyll-*a* contents of sediments at the end of the experiment. Furthermore, bacterial communities on leaf litter were also significantly affected by the presence of fungi. These results point to a major role of fungal communities in initial stream ecosystem functioning, well beyond their direct involvement in leaf litter decomposition.

## **5 Conclusion**

In conclusion, our observational and experimental investigations into the relationships between structural features in stream corridors, microbial communities, and C transformations revealed insights into the interdependencies between physical features and the structure and metabolism of stream microbial communities. In particular, we found for the open-land stage in the early successional landscape of the Chicken Creek Catchment that metabolic rates and

enzyme activities are surprisingly constant across the land-water interface and that hot moments are more important for C transformations than hot spots. Experiments revealed the significance of sediment disturbances on stream microbial communities and metabolism and the control of hyporheic metabolism by sediment structures that regulate the advective water supply of hyporheic biofilms. A feedback on water advection across the stream bed caused by the microbial metabolic products was also indicated. In experiments addressing the successional gradient from open-land to woodland stages we found indications for a major role of fungal communities in stream ecosystem functioning, beyond their involvement in litter decomposition. Furthermore, our results suggest that the type and density of terrestrial vegetation affect microbial community structure and function in streams, particularly enzyme production related to nutrient cycling. Overall, the variation of physical structures in stream beds and riparian zone during three successional stages had strong effects on microbial community structure and C transformations. Some of these findings may well apply beyond the early successional sand-bed streams studied in the Chicken Creek Catchment.

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## **Project C1 – Determination and modeling of water and matter balance in the artificially created catchment area “Huehnerwasser”**

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### **1 Introduction**

Water catchments are open dynamic systems with respect to mass, energy and momentum that strive towards an equilibrium status of development. Due to the open system character, balance equations are not closed solvable at the scale of catchments leading to the phenomena of equifinality of optimal parameter sets (Beven & Binley, 1992). The so called closure problem exists due to the generally unknown relationship between hydrologic state variables and fluxes (Troch et al., 2008). Finding the solution to the closure problem, if possible at all, is according to Beven (2006) the “Holy Grail” of scientific hydrology. Due to the controlled setup and known boundary conditions, the research at the Chicken Creek catchment is supposed to lead to more general explanations and understanding of general trends and patterns.

In the first phase of CRC/Transregio 38, the objective of C1 was to analyze the relationship between hydrologic state variables and fluxes as function of ecosystem development. This analysis was based on spatial measurements and simulations of water flow. To this end the research group of WSL had a focus on near-surface processes, whereas the BTU Cottbus group focused on groundwater dynamics. The initial hypothesis was that the seemingly homogeneous soil would allow simulating the water flow and residence with a classical model approach that assumes isotropic and easily measurable hydrological parameters. Further, it was hypothesized that the impact of marked structures in surface topography and vegetation would become significant with the subsequent development of the catchment.

### **2 Results**

Our observations and analysis of the catchment hydrology revealed that such a homogeneous initial state was never present, and thus, hydrological modeling on the assumption of isotropy was not appropriate. Structures and inhomogeneities showed up already in the very first autumn in 2005 and can be explained on the one hand by the slightly uneven topography after the build-up of the catchment on the other hand by soil structures originating from the way how the substrate was built (key word: *Schüttrippen*).

The emerging gullies have obviously played a very central role for the runoff behavior of the catchment. It was demonstrated that a numerical model with measured hydrological properties and observed groundwater level as lower boundary condition, but disregarding gullies failed to simulate surface runoff. However, the emergence of a pronounced gully network during the first years is a clear indication of surface runoff. Also, level changes in the pond during rainfall events suggested that 100 - 150 mm y<sup>-1</sup> run off immediately during and after rain storms – most probably in connection with surface runoff.

Hofer et al. (2011) developed a model to demonstrate that this immediate runoff may also be linked to the connectivity of hillslope elements in the catchment. The simulations showed that the degree of drainage pathway connectivity depends on small-scale variability of soil depth, soil hydraulic properties and topography. The connectivity of the system was found to be very sensitive to changes of soil water content in the catchment with dramatic change of subsurface flow for small changes in soil water content. This threshold-like behavior of flow paths connectivity accounted for the sudden availability of a large amount of drainable water, postulating a non-linear rainfall–runoff relationship as confirmed by first observations in the Chicken Creek catchment.

The gullies are crucial in understanding the hydrology of the Chicken Creek catchment as the hydrological properties of the gullies differ considerably compared to inter-gully areas. Therefore, the adequate simulation of the generation of the gully system is indispensable when modeling the hydrology. We developed and compared different model approaches to simulate the erosion rill network (Hofer et al., 2012): a) a self-organized critical network approach with soil erosion and sediment deposition governed by a local critical shear stress, and b) an approach based on the computation of particle transport as function of flow velocity determined by the Manning equation. Both models were able to qualitatively reproduce the observed main rill network. From this simulation we concluded that the mature rill network was largely the result of the very initial surface micro-topography of the catchment (supporting one of the main hypothesis stated above).

The results of this study were then used to develop a new spatially detailed three-dimensional hydrological model describing water transport in discrete volume units (Hofer, 2011). Different from other traditional hydrological models, this model simulated the emergent macro-scale patterns, as well as the non-linear threshold-like runoff-rainfall response, which was observed in the Chicken Creek. First simulations with the new model were able to reproduce realistic surface runoff patterns and transit times, as well as to simulate the temporal evolution of subsurface flow paths. They demonstrated the practicability of the new model concept and provide an encouraging basis for the further enhancement of the model.



The development of the groundwater system was characterized by filling the pore volume of the initially unsaturated sediment body until a dynamic equilibrium is reached. This equilibrium is a function of groundwater recharge, storage and losses from drainage and evapotranspiration. The initially observed trend of rising groundwater levels indicated a groundwater recharge higher than the losses. The observations suggested that the catchment only reached dynamic equilibrium in 2009, but in 2010 another groundwater level rise occurred due to a very wet summer. In general, the temporal behavior of groundwater measurements clearly reflected the influence of the seasonal dynamics of recharge and discharge on the groundwater table.

Assuming initial homogeneity and isotropy, a groundwater model was set up to simulate the groundwater flow behavior. Identified hydrogeological structures and flow patterns were iteratively implemented enhancing the model complexity. Here, too, the erosion gullies were detected as important catchment structures. Cutting into the aquifer and draining the groundwater body, the gullies are a crucial boundary condition for the modeling of the groundwater system.

The hydraulic conductivity was ascertained as one of the most sensitive model parameters. The permeability of the aquifer derived from soil texture analysis and hydraulic tests varied widely across the catchment. The generally low permeability impeded the groundwater flow and led to high groundwater levels. Furthermore, the taking of representative groundwater samples from the observation wells is hampered due to low hydraulic conductivity resulting in very low yield. The search of appropriate sampling techniques remains one challenge for the next phase.

### **3 Conclusions**

The research in phase 1 (sub-projects C1 and C2) allowed quantifying the water balance components for the transition from an initially empty soil water storage to a replenished groundwater body. This stage was reached after approximately three years. One water balance component, evapotranspiration, has increased over the years, not only because of the raising groundwater table, but also because of the emerging plant cover. With its well-defined boundaries and the comprehensive observation program, the Chicken Creek catchment seemed to offer the great opportunity to close the catchment water balance as discussed in Beven (2006). However, catchment heterogeneity and the lack of reliable measurement techniques impeded the determination of evapotranspiration and storage changes as integrated catchment water balance components so far. The catchment water balance could not as yet be closed and constitutes one of the ongoing challenges for further hydrological research projects at Chicken Creek catchment.

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## **Project C2 – A priori predictions in small catchment hydrology**

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### **1 Introduction**

#### **1.1 Research questions**

Subproject C2 focused on a priori predictions of hydrological responses of catchments. The purpose of catchment models in general is to predict the dynamics of state variables (such as mass, momentum and energy) and of mass and energy fluxes across its boundaries. With this in mind, the question was posed: How well can we predict hydrological responses based on different types and levels of information about the catchment? Both, a posteriori and a priori approaches were used to test modeling capabilities of conceptually different catchment models. We proposed to form an international cluster of hydrologists whose work focuses on the use and development of catchment models. This group was expected to collaborate on prediction of hydrological responses of the artificially constructed Chicken Creek Catchment. For the modelers it was a rudimentarily known black box. We planned a series of workshops to integrate and evaluate how the various a priori approaches could be used and implemented to model catchment responses. The ultimate clue of this exercise was to document the improvements of prediction quality with increasing availability of information about the initial status of the catchment.

#### **1.2 Modeling iterations**

In line with the proposal available models were identified, which were considered as being suitable for prediction in ungauged catchments. The “model-owners” or their collaborators were invited to predict the dynamics of the “Chicken Creek” for the first three years after construction of the catchment. The ten catchment models were conceptually quite different. Soil property data, topography, photographs of the gully network, initial water storage, vegetation coverage and weather were provided without any further information on discharge and evapotranspiration. At the first workshop the predictions were discussed. The catchment was visited only after this workshop. At the second workshop the modelers came up with a second prediction still based on the same input data but, this time, the discussion among the modelers and visual inspection of the catchment represented an increased a priori knowledge, an “improved intuition”.

During these two modeling iterations neither of the models came close to accurately predict the measured discharge nor evapotranspiration. Most models predicted discharge from the catchment as groundwater flow while in reality most water was discharged as surface runoff. This model inter-comparison highlighted the role of the model user in deciding how to parameterize the model based on the same information (Bormann et al., 2011; Holländer et al., 2009). This human aspect of modeling and prediction has therefore become an important aspect of the project. In a third step we then investigated the decision making processes and time allocation for making a third prediction based on much more detailed information – but in absence of calibration data. The costs of the additionally provided data were pro forma charged to the modeler.

## 2 Result

The main result gained in this modeling effort is the fact that the modelers prior experience and system understanding is at least as important if not more important relative to the increasingly detailed information and parameterization (Holländer et al., 2013).

Project related workshops

1<sup>st</sup> C2 Workshop „Hydrological Modeling Prediction – Chicken Creek“, December 1-2, 2008, Cottbus (13 presentations)

2<sup>nd</sup> C2 Workshop „Hydrological Modeling Prediction – Chicken Creek“, November 29-30, 2009 Cottbus (15 presentations)

3<sup>rd</sup> C2 Workshop „Hydrological Modeling Prediction – Chicken Creek“, September 24, 2010, Cottbus (11 presentations)

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## **Project C3 – Measuring and modeling surface structures as determinants and results of the primary succession of an ecosystem**

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### **1 Introduction**

Our proposal for the first phase of the CRC/Transregio 38 originally contained two intertwined research areas: 1) Descriptive analysis of surface and vegetation state and changes based on terrestrial laser scans, 2) Modeling the feedback between vegetation and surface development.

State of the art in terrestrial laser scanning (TLS) for ecosystem description purposes was and still is in an advanced development stage. Up to now TLS has not been used to gather data from ground vegetation and soil surface simultaneously. In most cases the vegetation is only seen as a confounding factor while trying to get surface elevation (terrain) data (Guarnieri et al., 2009; Perroy et al., 2010). Simulation models that cover either vegetation or terrain surface dynamics are widespread; however, only few models exist that take into account the feedback between both kinds of processes.

### **2 Results**

The first achievement was to find an alternative way to set up the scanner without causing any disturbance to plants or soil development. The original concept to put the scanner on a tower trailer was not feasible anymore, as access inside the Chicken Creek area is only allowed on stepping stones too small for trailers and outside access was prohibited by VEM. Theoretical calculations for the proposed scan resolution led to a minimum of 13 setup positions with a scanning height of about six meters. Thus, a transportable commercial telescope tower was rigged with a special foot to compensate for the inclination of the stepping stones and a specifically constructed head for mounting the laser scanner on top of the tower. Furthermore, a transportation and stabilizing system was developed to enable high precision scans.

All scans are aligned to the global reference coordinate system provided by VEM. For discerning vegetation and soil surface in the scan data (a point cloud of about 2.7 GB per campaign), special algorithms were developed. These include storage, preconditioning and processing modules. The results are a raster dataset with a resolution of 0.5 m x 0.5 m derived by means of moving window algorithms utilizing local minimum filters, total regression planes and loess algorithms. For each raster point data such as height, deviation, median and density of the points are available. With this approach, a digital elevation model and a digital surface model are generated simultaneously and represented as a raster dataset.

The first scan session was conducted in September 2008 and was repeated in February 2009, May 2009, August 2009, April 2010, October 2010, February 2011 and May 2011. From these datasets, the spread of vegetation in terms of its density and height in conjunction with the ongoing soil erosion (gully width, depth and length) (Fig. 1) can be assessed and used in the future as a source for model setup and parameterization. With these data, we were able to show, for example, that tree-like plants above 1.3 m height are spreading in the upper part of the catchment (2008: 23 plants, 2009: 51 plants), which means that the number of trees has more than doubled in this period, thus documenting the first phase of an accelerating colonisation by woody plants. The site-dependent mode of competition as investigated by Pretzsch & Biber (2010) is assumed to be a key factor in this process. Algorithms for automatic gully extraction and automatic calculation of indices for vegetation height and density have been developed.

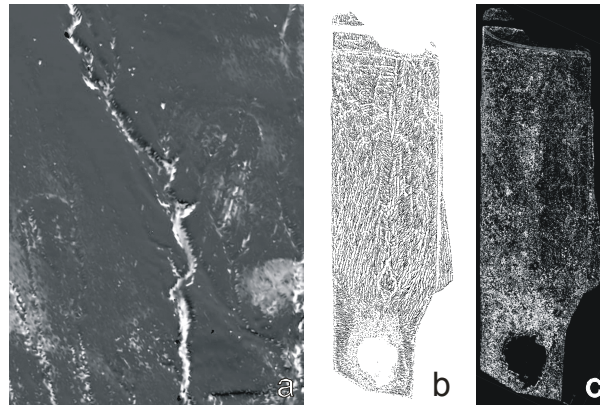


Fig. 1: Results calculated from 0.5 m x 0.5 m grids: (a) Erosion of the central gully 2009-2010 (b) Flow network April 2010 (c) Positive vegetation height changes from 2009 to 2010 (range 0 to 0.7 m).

Besides the scanning on Chicken Creek, detailed investigations on the interactions between the laser scanner and vegetation were conducted. On the Experimental Area, two plots were planted with *Robinia pseudoacacia* and *Pinus sylvestris* in different spacings. These plots were scanned to model plant density of the two species using the point distribution obtained from the scans. The same procedure was conducted in an experiment where 200 *Robinia pseudoacacia* and *Pinus sylvestris* seedlings were planted in small tubes. The plants were placed on a board in different densities and in different arrangements. Each combination was scanned, and a sub-sample of the seedlings was measured manually, dried and weighted. With this experiment, the relation between laser incidence angles, scan range, plant density and structural properties were recorded to have an empirical basis for models to estimate plant density and biomass for patches and stands of such young woody plants. Allometric rules are important biological backbones for such models (cf., Pretzsch, 2010).



As a first approach to simulating vegetation dynamics, a simple grid-based simulation model for the spatial dynamics of plant populations has been developed. The model is intended to be generic for annual plants and describes the typical patch formation of *Trifolium arvense*, which dominates parts of the Chicken Creek catchment, quite realistically with adapted parameter settings. The model is based on simple rules so far, and comprises algorithms for spatial seed spread, competition, growth, mortality, and spatial pattern evaluation. Technically, it is implemented in the free statistical programming language R that turned out to be very useful for developing and testing such a medium-sized model.

Catchment-wide data from the laserscan campaigns and from soil and groundwater measurements and vegetation monitoring as conducted in project Z1 have been analysed by Biber et al. (2013) in order to statistically scrutinize a set of hypotheses. These are related to the questions a) how far initial soil conditions determine future terrain surface structures, and b) how far surface and substrate characteristics determine plant species compositions, and c) how 3D vegetation structure influences terrain surface development.

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## **Project C5 – Development of a structure and process model**

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### **1 Introduction**

The project idea was to spatially integrate and analyze results of all individual subprojects such that the central hypotheses can be tested (i.e., the initial development phase controls the development and determines the later state of the ecosystem). Characteristic development phases could be better identified with the help of a spatially and temporally integrated 3D model. A structure and process model including compatible visualization tools was to be developed for integrating the dynamic and structure-related processes during the initial development phases. The model was intended to balance all system elements, masses, and components. From the structured data model, the parameters of the process models (e.g., hydrology) for the catchment should be derived. In turn, the results of the process models should be included in the 3D model (e.g., water table) and visualized in an integrative and comprehensive analysis for deriving system states and phases of the development.

The dynamic interactions between structures and processes are considered in many fields (e.g., cybernetic, ecology); and different types of structures are described depending on the scale and organization level (e.g., ecosystem, food web, population). Structures that are relevant for initial development of a hydrologic catchment are related to the spatial organization and composition of the solid phase (e.g., mineral or organic sediments, initially present biotic components).

In geological modelling, the dynamics of the solid phase structures was studied for describing soil production, erosion, and weathering rates considering mostly relatively large space and long time scales. Here, mass balance models (e.g., Anderson et al., 2002) were proposed using exponential relations for describing the soil production rate and constitutive relations between composition and physical properties of sediments (Brimhall & Dietrich, 1987; Heimsath et al., 1997). Distribution of soil thickness was modelled depending on climate and tectonic (Braun et al., 2001). These erosion models were verified using cosmogenic nuclides (e.g., von Blanckenburg, 2006). Effects of biota and organisms on structure development; however, were not well studied (Dietrich & Perron, 2006).

In soil landscape models, the long term development of spatial distribution of soil types in the landscape (e.g., Minasny & McBratney, 2006) and pedogenetic processes (Hoosbeek & Bryant, 1992) are quantitatively described. Earlier approaches to simulate pedogenesis were integrating the process models (i.e., water flow, solute transport, and other) directly while more recently, phenologic-genetic approaches tried to include morphological features in order to utilize the knowledge base from classifications and soil profile inspections (e.g., Galbraith & Bryant, 1998). Quantitative modeling of soil development in the landscape had to consider leaching, lateral sediment losses, and changes in particle sizes (Minasny & McBratney, 2006). The development of soil thickness in a complex agricultural landscape was mechanistically described with erosive and diffusive mass relocations at the soil surface with data from a digital elevation model and integrated in a cellular automata model (Follain et al., 2006). The partial differential equations can be solved by cellular automata (Wolfram, 1984; Crave & Davy, 2001) but also with classical numerical methods (e.g., Willgoose et al., 1991).

For the 3D-visualization of soil landscapes, graphic and computer-aided-design (CAD) programs, and specific software for soil science applications were developed (Delerue & Perrier, 2002). Grunwald et al. (2000) used the Virtual Reality Modeling Language (VRML), to generate 3D soil landscapes with spatially distributed soil horizons.

In hydrogeology, the reconstruction of spatial patterns and structures in models is currently regarded as one of the central challenges for improved descriptions of flow and transport (e.g., Schulz et al., 2006). These and other authors emphasize the importance of structure-related effects of internal heterogeneity and of feedbacks between flow and structure development. Non-invasive geophysical techniques are proposed to directly obtain soil structure information (e.g., Wendroth et al., 2006); in addition, the knowledge on structure forming processes could be utilized to interpolate and estimate soil hydraulic property distributions (Buczko et al., 2001). This latter strategy is a central aspect when trying to connect hydrology and pedology. In “hydrogeology” (Lin, 2003; Wilding & Lin, 2006), the formation of soil structure is quantitatively described in order to transform the structure information via “pedotransfer functions” into parameters of transport models. Predictive descriptions of soil structure change effects on water, solute, or energy budgets are rare, except, for instance, a topology- and connectivity-based approach on quantifying soil structure (Vogel et al., 2002).

In soil-hydrology, relations between soil surface and hydraulic properties by using transfer functions that include topographic characteristics have been proposed only recently (e.g., Leij et al., 2004). A full quantification of soil structural features such as degree of aggregation is still limited. Proposed was a relative morphometric index (Lin et al., 1999) that varied between 0 and 1 and allowed estimating structure parameters from field observations. Soil erosion in a rill network showed a complex feedback between network development and overland flow or sediment transport (Brunton & Bryan, 2000).

In soil biology, changes in the soil structure following the invasion of a new earthworm species were reported explained by differences in feeding and burrowing activities between the native and the invaded worm species (Hale et al., 2005). The secondary effects of structure changes on hydraulic properties and water budgets have not been studied here; however, some main may be assumed from the structure changes. In analogy to structural changes in the initial phase of soil organisms and plant root development, similar feedbacks can be expected (e.g., van Genuchten & Simunek, 2004).

Here, the basic questions were how to construct a 3D structure model and how to integrate the information in space and time in a way that an integrative analysis of the ecosystem development in the catchment across all sub projects was possible. Geo-referenced spatial information on sediments and other components had to be combined in a way that allowed a 3D visualization and balancing. Based on these distributed properties and structures, regions with predominating relevant processes (“spatial process domains”) should be defined and model parameters derived. Ecosystem development due to structural changes should be described. Based on the integrated modeling approach, C5 was also involved in improving the data exchange and communication.

## **2 Results and developed methods**

The first project period focused on the development of 2D surface and 3D catchment structure models to quantify sediment mass distribution for times when aerial photographs were available. Soft- and hardware and the available data were acquired and evaluated including model conceptualization. The geological 3D modeling software GOCAD (Suite 2.5.2., Paradigm Ltd.) was found to be a suitable tool for our purpose because it offered adequate functionality and flexibility, and allows sharing the 3D visualization with other groups. The 3D catchment models can be viewed by all other groups with “Geocando”, a publicly available viewer (<http://www.softpedia.com/get/Multimedia/Graphic/Graphic-Viewers/Geocando.shtml>).

### **2.1 Reproduction of the initial mass and structure of the sediments**

The reproduction of the initial mass and structure of the sediments (solid phase) using GOCAD started with identifying spatial configuration of upper and lower boundaries of the artificial catchment (i.e., clay base liner, initial soil surface). Triangulated (TIN) digital elevation models (DEMs) of the catchments surface and subsurface delineation were constructed based on data from digital photogrammetry and boreholes. The subsurface and surface catchment areas for defining the watershed boundaries were delineated using the D8 flow accumulation algorithm in SAGA GIS.

Once the limiting surfaces were established, a gridded 3D-representation (volume model or stratigraphic grid (SGrid)) of the sediment body was constructed. Initial sediment volume was about 120,000 m<sup>3</sup> ( $\pm$  12,000 m<sup>3</sup>) for a mean thickness of about 2 m. DEM quality has been assessed and improved by integrating d-GPS elevation data. The results such as surface and subsurface catchment boundaries were used in the modeling workshop (C2), and distributed among all groups within the CRC/Transregio 38 in form of 2D and 3D data sets, including project documentations. From differential surface DEM maps derived from aerial photos at different times and measured data of bulk densities (nested sampling campaign led by A3) the spatially distributed mass changes were obtained. For example, this analysis estimated a sediment mass movement of more 3,100 t between 2005 and 2008 (Fig. 1).

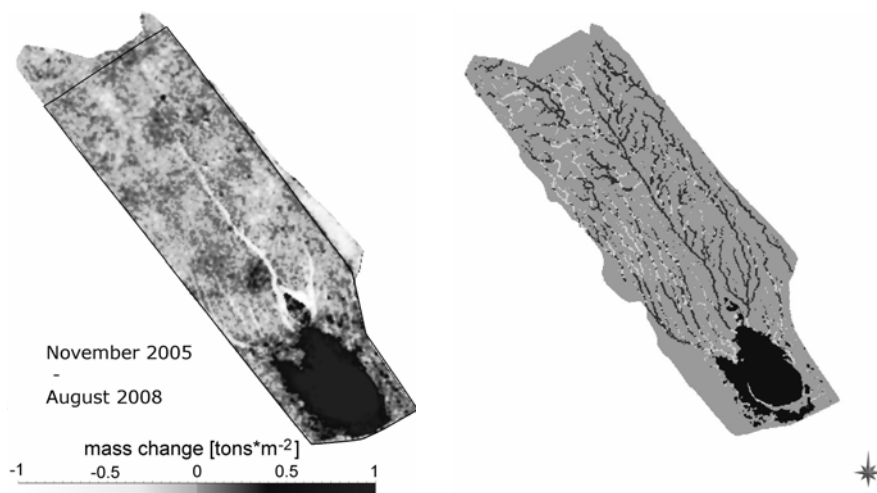


Fig. 1: (left) spatial distribution of local sediment mass changes between November 2005 and August 2008 (dark is accumulation and light is depletion) and (right) geo-morphodynamic sub-regions with darker areas indicating lower elevation (e.g., rills) and a topographic wetness index of more than 7).

## 2.2 Impact of wind erosion on the sediment balance

Since the potential impact of wind erosion on the sediment balance and structural dynamics during the initial period (Sept. 2005-February 2008) was unknown, the sediment transport via wind was estimated using the Wind Erosion Prediction System (WEPS). The significance was studied in a multi-scenario modeling approach. Input parameters for WEPS were derived from measured soil properties of the raster sampling, from weather station data (Z1), from visual observations and photos, and specific parameters were estimated from experience gained in previous work on sites with comparable bare surface conditions (Maurer et al., 2009; 2010). Simulation results were partially verified using aerial image analysis. The results show that material redistribution caused by aeolian processes is in the magnitude of hundreds of tons in the 2 year simulation period (about 10 t ha<sup>-1</sup> a<sup>-1</sup>) and localized at the surface of certain areas.

Surface conditions assumed for scenarios with relatively high erodibilities seem to be most realistic. However, the magnitude of interaction between wind and water erosion still remains unclear.

### **2.3 3D volume models**

Multi-temporal gridded 3D volume models were constructed from the delineating subsurface and surface DEMs (Fig. 2). Physical and chemical soil properties from borehole sampling (A2, Z1) were assigned to the cells of the volume model after interpolation by Ordinary Kriging, following a 3D analysis of spatial variability of the soil properties. For quantifying the initial sediment budgets in defined time intervals, 3D sediment redistribution was reconstructed for the days with available surface elevation data. The 2D surface and 3D volume models for defined times were further subdivided in regions of differing surface structural characteristic or morphodynamic and used for separately evaluating DEM quality and sediment budgets. The viability of elevation data from digital photogrammetry, airborne laser scanning, and ground based laser scanning (C3) was assessed in a comparative study. Plausibility rules were used to modify the surface elevation data from digital photogrammetry and ground based laser scanning for an improved quantification of sediment budgets. (e.g., correction of drainage network's longitudinal elevation profiles according to hypsography). The methods have been evaluated by comparing DEMs with d-GPS field data and by sediment budgets. Reconstruction of initial sediment relocations could be improved using the modified DEMs. Topographical parameters were derived from the DEMs and a surface drainage network was extracted. Automated extraction of surface drainage networks and other structural characteristics was limited by DEM accuracy and resolution and required additional digitalization from aerial photographs. Surface topography responded first and most intensely to external forcing during the initial stage. The first assessment of the initial structural dynamic was focusing on the development of surface topography.

### **2.4 Depositional sediment structures**

Catchment-internal depositional sediment structures are presumably governing many aspects of early ecosystem development. The fundamental layout of the internal structural elements (spoil ridges) was derived from aerial photographs and specific sediment volumes and masses were calculated from DEMs based on photogrammetric surveys. Information on sediments of the excavation site (e.g., texture, spatial settings of geological units) was obtained from Vattenfall Europe Mining AG. The internal structural elements (i.e., spoil ridges) are supposed to have a considerable impact on hydraulic parameters and transport processes. Spoil cones located in the open-cast mining area were sampled to validate theoretical studies about their internal heterogeneity.

For this purpose, 3D-representations of two sampled spoil cones were constructed in GOCAD and the point data were interpolated using the GOCAD 3D Discrete Smooth Interpolation (DSI) Algorithm. A central compacted zone within each spoil cone resulting from the dumping process was found. Soil bulk densities found in the spoil cones (which were not bulldozed or compacted otherwise) ranged from 1.3 - 1.6 g cm<sup>-3</sup>. However, particle size variability resulting from segregation processes could not be detected because the sampling method was not detailed enough. As above, physical and chemical soil properties from borehole sampling were assigned to grid cells of the volume model after interpolation by Ordinary Kriging; however, the resulting distribution of initial internal heterogeneities appeared to be not useful.

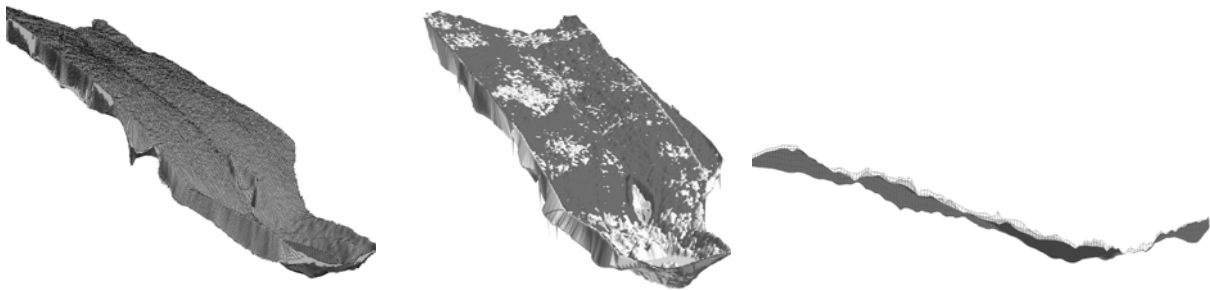


Fig. 2: (left) 3D volume body as initial condition (Nov 2005), (centre) spatial distribution of newly formed surfaces (white: increase till June 2009) from sedimentation (grey: initial surface, Nov 2005), and (right) vertical cross-section (left-to-right) through the lower part of the catchment, with additional sedimentation layers till Nov 2007 (darker grey) and Aug 2008 (light grey).

Thus, a mechanistic model was developed to generate the internal heterogeneities: A structure generator program using Visual Basic for Applications (VBA) that simulates a series of 2D-cross sections through spoil cones based on preliminary work (Buczko et al., 2001) and by incorporating information on sediment composition and spatial layout of spoil ridges (Fig. 3). Spoil cone geometry (i.e., slope angles, horizontal distances, height, position on the spoil ridge, azimuth according to ridge orientation, distance from cross section to cross section) is calculated according to the specified conditions. Each spoil cone has a compacted central part with relatively higher bulk densities. Simulated segregation processes result in soil texture differentiation within layers oriented along the spoil cone flanks. Initial sediment composition is currently based on “mixing” a mean texture proportional to sediment layer thickness at the excavation side. The mixing is randomly modified for the hierarchical levels of a spoil ridge section, an individual cross-section, and an individual layer. A digital representation of the excavation site simulating excavation and transport processes on the conveyor belt provides “packages” of mixed mean sediments. Mineralogical information will be added in the next development stage.



The structure generator creates distributed texture (skeleton; fine, medium, coarse sand; silt; clay) and bulk density data in selected resolutions. The data can be imported into GOCAD, and assigned as property values to individual cells in the catchment's volume body.

The results are digital representations of generated spoil ridges of the eastern half of the catchment (7 cm x 7 cm resolution in cross sections and 3 m distance from next cross-section). For the catchment, the individual spoil information is spatially aggregated and properties are interpolated before being combined with a volume body.

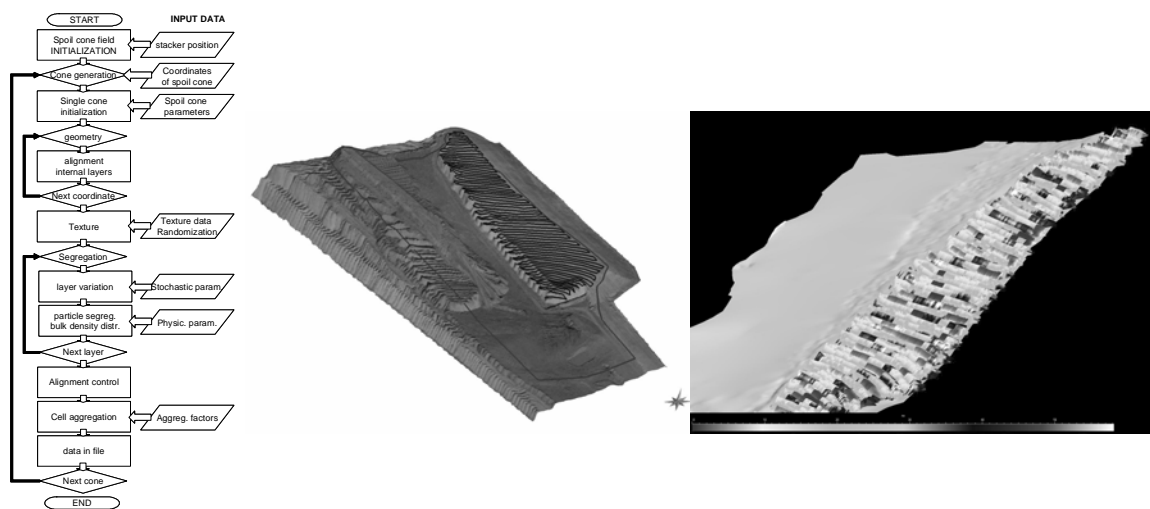


Fig. 3: (left) flow chart of structure generator, (centre) sediment deposition trajectories depending on stacker position, (right) spoil ridge representations from the structure generator visualized in GOCAD.

### 3 Conclusions

There are a number of related approaches (presented in the first proposal in more detail) that were developed in the fields of geosciences, pedology, hydrology; also visualization tools for 3D soil landscape models (e.g., virtual reality modeling language). The novel aspect of the proposed work here is the explicit inclusion of a 3D solid (mineral, organic, organisms) phase structure and mass balance and the definition of process domains (i.e., complex 3D structure and process model).

Concepts regarding structure modeling can be found in geomorphology where landscape evolution models are being developed (e.g., LAPSUS, University of Wageningen). However, these models cover longer time periods and are not including initial development phases (e.g., Temme & Veldkamp, 2009).

Relatively comparable approaches based on a structure generator were recently presented (Miller et al., 2008; Michael et al., 2010). These authors developed a (geologically) realistic spatial model of structural heterogeneity conditional to available structural data. The output of a process model (i.e. a structure generator) is used as a data base for statistical and deterministic rules combined to produce a 3D-model of heterogeneity that closely approximates that of the model.

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