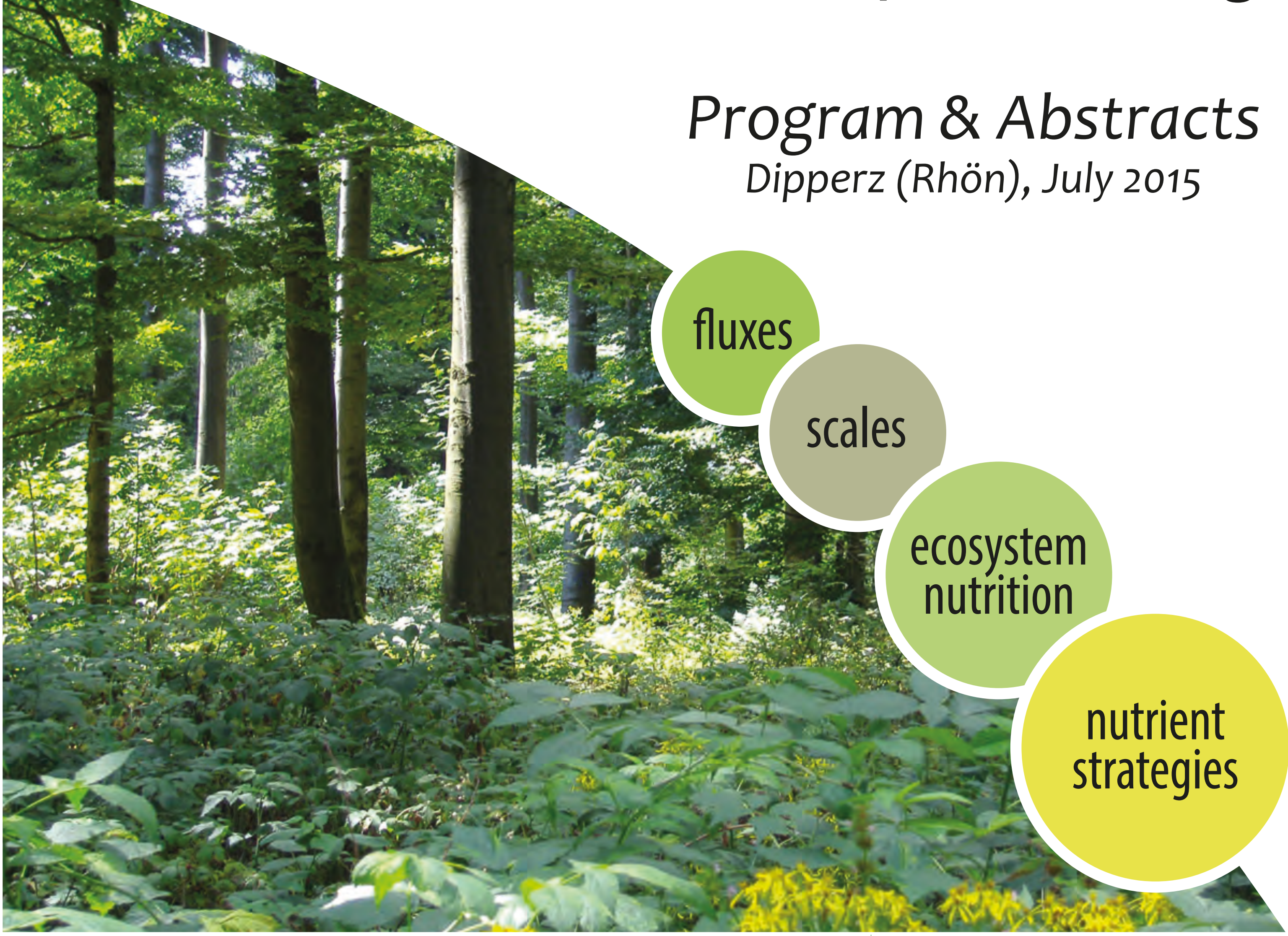
SPP 1685

Ecosystem Nutrition 2015

Status Workshop & Meeting

Program & Abstracts

Dipperz (Rhön), July 2015



fluxes

scales

ecosystem nutrition

nutrient strategies

Welcome to

SPP 1685

Ecosystem Nutrition

2015

Wednesday, July 1

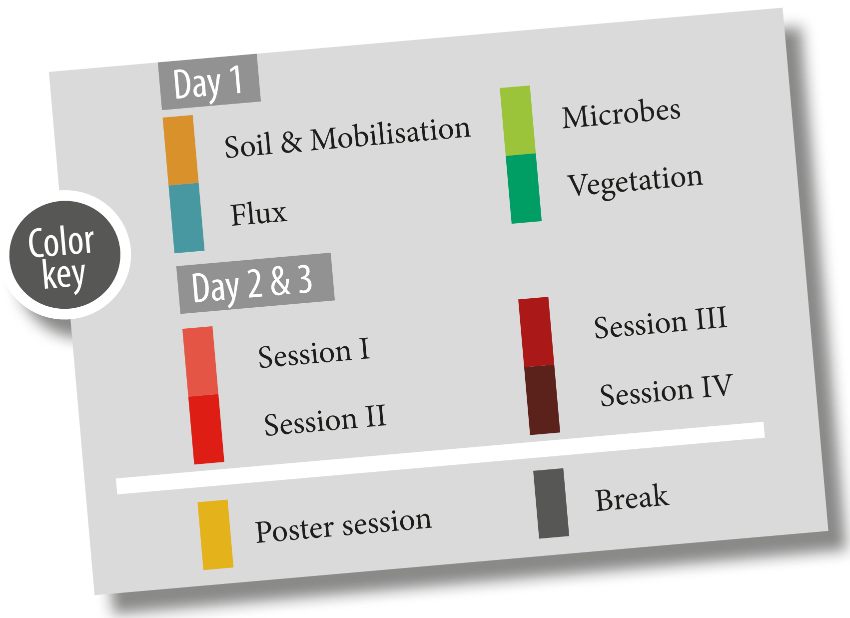
8:45–9:00	**Welcome and Introduction**	**Friederike Lang** *(Universität Freiburg)*
9:00–9:15	**Review: Cluster Soil and Mobilisation**	**Friederike Lang** *(Universität Freiburg)* **Jörg Luster** *(WSL Birmensdorf)*
9:15–9:35	P dynamics along availability gradient of the SPP 1685 sites, as revealed by isotopes (^{33}P and ^{18}O in phosphate) in the gield and in incubation experiments	**Chiara Pistocchi** *(ETH Zürich)*, Federica Tamburini, Éva Mészáros, Else K. Bünemann, Emmanuel Frossard
9:35–9:55	Soil minerals as control for the phosporus status of forest ecosystems: Combining field and laboratory evidence	**Marc-Oliver Göbel** *(Universität Hannover)*, Robert Mikutta, Jens Boy, Georg Guggenberger
9:55–10:10	**Review: Cluster Flux**	**Frank Hagedorn** *(WSL Birmensdorf)*
10:10–10:30	Phosphorus concentrations in runoff and interflow at the sites Conventwald, Vessertal and Mitterfels	**Jakob Sohrt** *(Universität Freiburg)*, Heike Puhlmann, Markus Weiler
10:30–10:50	Phosphorus of colloidal forest soil fractions as revealed by Field Flow Fractionation	**Anna Missong** *(FZ Jülich),* Roland Bol, Volker Nischwitz, Jan Siemens, Erwin Klumpp
10:50–11:20	*Coffee*	
11:20–11:35	**Review: Cluster Vegetation**	**Arne Cierjaks** *(Universität Hamburg)*
11:35–11:55	Phosphate nutrition of host plants in ectomycorrhizal symbiosis	**Uwe Nehls** *(Universität Bremen)* and Annette Hintelmann
11:55–12:10	**Review: Cluster Microbes**	**Stefanie Schulz** (Helmholtz Zentrum München), **Michael Schloter** (TU München)
12:10–12:30	Phosphatase activity in soils and in the rhizosphere of *Fagus sylvatica* as dependent on site, P availability, and season	Kerstin Hofmann, Christine Heuck, **Marie Spohn** *(Universität Bayreuth)*
12:30–13:30	*Lunch*	
13:30–15:00	Poster session	
15:00–15:30	*Coffee*	
15:30–18:30	Workshop	
18:30–	*Dinner*	

Thursday, July 2

9:00	Idea and research concept of the priority programme „Ecosystem Nutrition“	**Friederike Lang** *(Universität Freiburg)*
9:30	***Invited talk:*** The challenge of recognizing microorganisms as key players in ecosystem nutrition	***Benjamin L. Turner*** *(Smithsonian Tropical Research Institute, Panama)*
10:15	The relativ importance of soil organic phosporous mineralization in mineral topsoil under beech forest is greatly affected by the availability of inorganic phosphorous	**Else K. Bünemann** and Salome Augstburger *(ETH Zürich)*
10:35	Do microbial carbon use efficiency (CUE) and the mean residence time (MRT) of microbial biomass C depend on soil stoichiometry?	**Marie Spohn** *(Universität Wien / Universität Bayreuth)*, Karoline Klaus, Wolfgang Wanek, Andreas Richter
10:55	*Coffee*	
11:25	Phosporus deplretion in forest soils shapes bacterial communities towards phosporus recycling systems	**Fabian Bergkemper** *(Helmholtz Zentrum München)*, Marion Engel, Friederike Lang, Michael Schloter, Stefanie Schulz
11:45	Composite plants: a versatile tool for promotor analysis in ectomycorrhizal symbiosis	**Dimitri Neb** *(Universität Bremen)*, Maria Grams, Uwe Nehls
12:05	***Invited talk:*** Phosphorus mobilization from forest soils by ectomycorrhizal fungi: recent data and actual role	***Claude Plassard*** *(INRA Montpellier, France)*
12:50	Ectomycorrhizal communities in relation to a phosporus gradient	Aljoša Zavišić, Pascal Nassal , Marie Spohn, Ellen Kandeler, **Andrea Polle** *(Universität Göttingen)*
13:10	*Lunch*	
14:15	**Walk & Talk**	
15:00	A novel ^{33}P labelling approach: Competition between roots and microorganisms for phosphorus	**Thomas Zilla** *(Universität Göttingen)*, Aljoša Zavišić, Michaela Dippold, Andrea Polle, Yakov Kuzyakov
15:20	Do interannual variations of phosporus contents in tree rings of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) reflect temporal variations in P avalability?	**Jürgen Bauhus** *(Universität Freiburg)*, Jörg Niederberger, Martin Kohler, T. Jaumann, E. Tress, Peggy Bierbass, Adrian Wichser, Heinrich Spiecker, Thomas Rötzer
15:40	*Coffee*	
16:10	Phosporus acquistion, storage, an mobilization in beech and poplar trees during annual growth	Florian Netzer, Ursula Scheerer, Heinz Rennenberg, **Cornelia Herschbach** *(Universität Freiburg)*
16:30	Effects of acidification by nitrogen input and liming on the P_{ortho} concetrations in soil solution	**Stefan Holzmann** *(FVA Freiburg)* and Klaus von Wilpert
16:50	Perspectives of microdialysis for analysis of phosphate availability in soils	Dominic Demand, **Helmer Schack-Kirchner** *(Universität Freiburg)*, Friederike Lang
17:10	Small Aggregates as temporary storage of P in forest soils?	**Simon Stahr** *(Universität Freiburg)*, Simon Haberstroh, Markus Graf, Robert Mikutta, Friederike Lang
17:30	Investigating patterns of phosporus speciation in soil aggregates by combining NanoSIMS, µXRF, and µXANES	**Florian Werner** *(TU München)* and Jörg Prietzel
17:50		
18:30	*Dinner*	

Friday, July 3

9:00	***Invited talk:*** Long-term and large-scale macronutrient modeling in terrestial ecosystems	**Ed Tipping** *(Centre for Ecology & Hydrology, Lancaster, UK)*, Jessica A.C. Davies, Edwin C. Rowe, John F. Boyle, Elisabeth Graf-Pannatier, Vegard Martinsen
9:45	Phosporus in Forest Stream Waters - The Relevance of Nanoparticles and Colloids	**Nina Gottselig** *(FZ Jülich)*, Volker Nischwitz, Thomas Meyn, Cynthia Halle, Roland Bol, Harry Vereecken, Wulf Amelung, Jan Siemens, Erwin Klumpp
10:05	Isotope geochemical determination of phosporus weathering sources and fluxes in forest ecosystems	**David Uhlig** *(GFZ Potsdam)*, Friedhelm von Blanckenburg, René Kapannusch
10:25	*Coffee*	
11:00	Is lateral subsurface flow the missing sink of P in mountainous forest ecosystems?	**Markus Weiler** *(Universität Freiburg), Jakob Sohrt*
11:20	Dissolved organic phosphorus (DOP) and its potential role for ecosystem nutrition	**Dominik Brödlin** *(WSL Birmensdorf)*, Frank Hagedorn, Klaus Kaiser
11:40	Poster session	
12:30	*Lunch*	
13:30	***Invited talk:*** Do ecosystems have nutritional strategies? A tale of two forests	**Cindy Prescott** *(University of British Columbia, Canada)*
14:15	Nitrogen cycling in forest ecosystems in changing climate	**Heinz Rennenberg** *(Universität Freiburg)*
15:00	Land-use impact on phosporus fractions in tropical soil in Sumatra Indonesia	**Deejay Maranguit** *(Universität Göttingen)* and Yakov Kuzyakov
15:20	Phosporus P nutrition types of forest ecosystems: First results on functioning and diagnostic properties	**Friederike Lang** *(Universität Freiburg), Jaane Krüger*
15:40	*Coffee + Wrap up*	
17:00		



Poster session

P 1	The importance of fungal-fungal and bacterial-fungal interactions for phosphorus dynamics in forest soils	**Pascal Nassal** *(Universität Hohenheim)*, Sven Marhan, Ellen Kandeler
P 2	The isotope signature of subsoil P – evidence of different bioaccessibility?	**Andrei Rodionov** *(Universität Bonn)*, Sara Bauke, Margaux Simon, Federica Tamburini, Sabine Willbold, Friederike Lang, Hans Lewandowski, Wulf Amelung
P 3	Microbial biomass stoichiometry and mineralization of organic carbon, nitrogen and phosphorus	**Christine Heuck** *(Universität Bayreuth),* Alfons Weig, Marie Spohn
P 4	Epigenetic adaption and memory in Populus trichocarpa	**Brigitte Schönberger** *(Universität Hohenheim)* and Uwe Ludewig
P 5	Phosphorus fractions in preferential flow pathways in forest soils	**Dorit Julich** *(TU Dresden)*, Maximilian Kirsten, Karl-Heinz Feger
P 6	Sugar efflux in Picea abies ectomycorrhizas	**Maria Grams** *(Universität Bremen)* and Uwe Nehls
P 7	Potential bioavailability of nanoparticulate and colloidal bound P	**Jan Wolff** *(FZ Jülich),* Nina Gottselig, Dominik Brödlin, Christian von Sperber, Jan Siemens, Erwin Klumpp
P 8	Humus form specific relationships between water extractable phosphorus (P), microbial biomass P and P mineralization rates in the forest floor and foliar P contents of European beech	**Dan Zederer** *(NW-FVA Göttingen)* and Ulrike Talkner
P 9	Seasonal analysis of P uptake and ectomycorrhizal diversity in young beech trees	**Aljoša Zavišić** *(Universität Göttingen)*, Nan Yang, Pascal Nassal, Marie Spohn, Rodica Pena, Ellen Kandeler, Andrea Polle
P 10	Biologically-released phosphate in soil under young beech trees (Fagus sylvatica L.) at two sites differing in soil P availability	Yvonne Oelmann, Thomas Pütz, **Simon Hauenstein** *(Universität Tübingen)*
P 11	Plant-induced chemical properties in the rhizosphere of Fagus sylvatica seedings depending on soil P speciation and tree provenance	**Sonia Meller (WSL Birmensdorf)**, Beat Frey, Emmanuel Frossard, Marie Spohn, Jörg Luster
P 12	Factors controlling P mobility in the soil under a beech stand	**Theresa Löffler** *(Universität Freiburg)*, Jaane Krüger, Friederike Lang
P 13	Are phosphorus patterns in forest soils influenced by the distance from European beech and Norway spruce stems?	**Moritz Melchior (Universität Freiburg)**, Jaane Krüger, Friederike Lang
P 14	The interplay of biodiversity and phosphorus in temperate forests – insights from a database analysis, a field study, and a greenhouse experiment	**Isaak Rieger** *(TU Berlin)*, Nicole Wellbrock, Daniel Ziche, Ingo Kowarik, Arne Cierjacks
P 15	Arbuscular mycorrhiza along forest soil sequences differing in P-availability	**Josef Kohler** *(FU Berlin)* and Mathias Rillig

List of participants

Amelung	Wulf	Univeristät Bonn (Germany)
Bauhus	Jürgen	Universität Freiburg (Germany)
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Brödlin	Dominik	WSL Birmensdorf (Germany)
Bünemann-König	Else	ETH Zürich
Cierjacks	Arne	Universität Hamburg (Germany)
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Wednesday, July 1

Oral presentation

P dynamics along the availability gradient of the SPP 1685 sites, as revealed by isotopes (^{33}P and ^{18}O in phosphate) in the field and in incubation experiments

Chiara Pistocchi, Federica Tamburini, Éva Mészáros, Else K. Bünemann, Emmanuel Frossard

Group of Plant Nutrition, D-USYS, ETH Zurich, Eschikon 33, 8315 Lindau, Switzerland

The main hypothesis of the SPP 1685 program "Ecosystem Nutrition: Forest Strategies for limited Phosphorus Resources" is that phosphorus (P) forms and availability in soils drive forest ecosystems from mobilisation of P from mineral phases (acquisition) to efficient biological cycling (recycling). Assessing the relevance of inorganic and biological processes requires the use of appropriate approaches and tracers. Soils were sampled in May and October 2014 from three forest sites chosen along the studied P availability gradient (Lüss, Vessertal, and Bad Brückenau). First, vegetation and soil P pools (resin, hexanol, $NaHCO_3$, NaOH, and HCl-extractable P) were characterized and thoroughly quantified. Resin-, hexanol- and HCl-extractable P were also analysed for the stable isotope composition of oxygen in phosphate (^{18}O-P), which is sensitive to biological processes.

Phosphorus concentrations of all pools clearly confirm the P availability gradient. Oxygen isotopes in phosphate give a more complex picture: contrary to previous observations (Tamburini et al., 2012), resin-P and hexanol-P show values generally lower than the expected temperature-driven equilibrium, with soils from Lüss deviating more from equilibrium. As a trend, ^{18}O-P values are lower and less variable in the hexanol-P compared to the resin-P pool. In addition, both are lighter in soils sampled in October than in May. Phosphorus extracted from fresh leaves shows the expected high ^{18}O-P values (Pfahler et al., 2013), while ^{18}O-P in litter is lower compared to the fresh leaves, but greater than soil P pools.

To better determine and understand the fluxes between vegetation and soil pools, and the processes driving them, radioactive (^{33}P) and stable isotopes (^{18}O-P) are currently used in controlled incubations. The organic horizon of soils from Lüss and Bad Brückenau (low *vs* high P availability and non-equilibrium *vs* equilibrium ^{18}O-P values) with and without the addition of leaf litter are incubated and sampled at different time points. P concentrations, ^{18}O-P, and ^{33}P are measured in soil pools obtained by a simplified sequential extraction. In parallel, respiration and the activities of the most important phosphoenzymes are measured. The results from the first extraction dates confirm the greater importance of biological processes in P dynamics in the P-poor soil, both in terms of relative size of the microbial P pool compared to the others (e.g. water- and resin-extractable) and in terms of fluxes (i.e. high immobilization rate compared to the P-rich soil).

References

Tamburini F et al. 2012. Environmental Science & Technology 46: 5956-5962
Pfahler V et al. 2013. New Phytologist 197: 186-193

Soil minerals as control for the phosphorus status of forest ecosystems: Combining field and laboratory evidence

Marc-Oliver Göbel[1], Robert Mikutta[1,2*], Jens Boy[1], Georg Guggenberger[1]

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Sorption of phosphorus (P) compounds to pedogenic minerals like Fe and Al (hydr)oxides is considered as an effective sink for P in forest ecosystems. However, it is currently poorly understood if there is a mineral control in both P-rich "acquiring" and P-poor "recycling" forest ecosystems or whether the mineral phase in these soils differently retains P and therefore constrains the P supply to microorganisms and plants. Such mineral-P associations may form by adsorption of P compounds to reactive minerals or by coprecipitation with hydrolyzable metals. However, the sorption affinity of various inorganic and organic P compounds for different minerals in comparison to their coprecipitation behavior with hydrolyzable metals is largely unknown. The same holds true for the mechanisms and extent by which microorganisms can extract also these hard-to-exploit P sources.
In order to address these questions, we followed two approaches during the first project phase: the first one was associated with the identification of P-mineral relationships in the core soils of the priority program, which represent a gradient in P availability. The second part involved a range of laboratory experiments which focused on the interaction of various P compounds with minerals and metals and the potential P release by model exudates. Relying on the central sites, we determined the fraction of organic and inorganic P associated with the mineral phase following density treatment and analyzed to which extent pedogenic Fe and Al (hydr)oxides are involved in the retention of P along the soil P gradient. In the laboratory studies, we determined the adsorption properties of Fe and Al oxides for various P monomers and polymers (orthophosphate, glucose-6-phosphate, phytic acid, RNA, extracellular polymeric substances, or dissolved organic P) as well as the coprecipitation of P forms with Fe and Al. The potential release of P from Fe oxides and coprecipitates was tested in batch dissolution experiments using different non-iron-reducing (oxalate) and iron-reducing (ascorbate and the siderophore desferrioxamine B; DFO-B) model exudates. The field data and laboratory results will be presented and supplemented by an outlook to running incubation and mesocosm experiments testing the ability of microbial communities to utilize mineral-associated P sources.

Phosphorous concentrations in runoff and interflow at the sites Conventwald, Vessertal and Mitterfels

Jakob Sohrt[1], Heike Puhlmann[2], Markus Weiler[1]

[1]*Chair of Hydrology, University of Freiburg*
[2] FVA Freiburg

Phosphorous concentrations in runoff- and interflow samples of the three sites were measured using the persulfate digestion method according to EPA ESS 310.2 and a semi-automatic photometer. For the site Conventwald reactive P in runoff was measured for two months parallel to the persulfate digestion method.

Temporal resolution is one day for the sites Mitterfels and Vessertal and 4 - 6 hours for the site Conventwald. Inteflow samples consist mainly of bulk samples though some interflow events have been sampled with high temporal resolution.

The P concentrations of the analyzed samples differ considerably between sites, runoff and interflow at each and show a high temporal variability. The temporal variability of P concentrations in streamflow is highlighted by data from an online photometer for reactive P which is placed at a weir at the catchment outlet of the Conventwald site and analyzes reactive P in 20 minute time steps.

For all three sites, P concentrations in interflow from the litter layer (0 - 20 cm soil depth) can be as much as two orders of magnitude higher than P concentrations in streamflow of the respective site. P concentrations in interflow from deeper layers are considerably lower and are close to those of runoff for the lowest layer (150 - 300 cm soil depth).

Phosphorus of colloidal forest soil fractions as revealed by Field Flow Fractionation

Anna Missong[1], Roland Bol[1], Volker Nischwitz[2], Jan Siemens[3] and Erwin Klumpp[1]

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[3]Institute of Crop Science and Resource Conservation, Soil Science and Soil Ecology, University of Bonn, Bonn, Germany

Natural nanoparticles (NP: diameter: 1-100 nm) and colloids (NC: diameter: 100 nm- 1 µm) are the smallest natural particles in soils. They exert a decisive control on the mobility and bioavailability of strongly sorbing compounds such as P due to their surface charge and high specific surface area.
In framework of the DFG-SPP 1685 on ecosystem nutrients we investigated the NC & NPs present in forest soils focussing on their role in the P cycling. Different sources of NC & NPs were analysed. Within the SPP central project of "Quantitative Pits" water dispersible colloids (WDC) in a size range < 500 nm were extracted from the depth profiles in the soils from the four SPP forest sites. For the subproject on mesocosm scale soil column experiments (FVA-Freiburg) we quantified the NC & NPs in leachates from forest soil column experiments.
We analysed the nanoparticles and colloids by Field Flow Fractionation (FFF) coupled to UV-, DLS-, OCD- detectors and inductively coupled plasma mass spectrometry (ICP-MS). The technique enabled a size resolved characterization of the colloidal and nanoparticulate fractions and their elemental composition (C_{org}, P, Si, Fe, Al, Ca, Mn).
The results did confirm that P in these forest soils was strongly associated to the NC & NP fraction. However, the amounts and composition of soil nanoparticles and colloids differed between the forest site and sample depth in the profile. The NC & NP s could be helpful in assessment whether a forest ecosystem is acquiring or recycling P. The soil leachate results did indicate that NC & NP, especially colloidal-P were vertically transported. Overall, 50 to 90 % of the P in the soil leachates was colloidal-P. Attention should be given to quantification of colloidal-P in P cycling studies.

Phosphate nutrition of host plants in ectomycorrhizal symbiosis

Uwe Nehls, Annette Hintelmann

Department of Biology and Chemistry, University of Bremen

Ectomycorrhizas (ECM) are specialized structures formed during the interaction of fine roots of woody plants with certain soil fungi. Improved nourishment of both partners under nutrient and carbohydrate limiting conditions is expected to be the driving force for this type of symbiosis.
ECM based phosphate nutrition of trees is essential for the success of boreal and temperate forest ecosystems. Understanding the molecular mechanisms of ECM fungal phosphate import, transport, and metabolism is thus necessary for a prediction of future tree nutrition. While phosphate import by Basidiomycotic fungi has been well investigated in the past, we have an only poor knowledge about cellular P metabolism, storage, as well as transport within the fungal colony. Furthermore, the mechanisms of fungal P export at the functional interface of ectomycorrhizas are completely unknown. We therefore started to address the question, whether ECM fungal homologs of the PhoI gene family of plant Pi exporters can be responsible for fungal Pi export in symbiosis. In plants, members of the PhoI gene family are involved in Pi excretion from parenchyma cells into xylem vessels.
Sequence analysis of fungal genomes revealed the presence of PhoI homologs in the genomes of Asco- and Basidiomycotic fungi. In the genomes of *Laccaria bicolor* and *Amanita muscaria* only single members of the gene family were found. Large scale transcript sequencing (RNAseq) revealed an about 5-times higher level of fungal PhoI transcripts in mycelia of ectomycorrhizas compared to hyphae grown in axenic culture. Reinvestigation of gene expression is currently under progress for ECM fungal models and will be presented together with a detailed analysis of gene expression under different nutritional regimes.

Phosphatase activity in soils and in the rhizosphere of *Fagus sylvatica* as dependent on site, P availability, and season

Kerstin Hofmann, Christine Heuck, Marie Spohn

Department of Soil Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University Bayreuth, Germany

The rhizosphere is a thought to be a hotspot of organic phosphorus (P) mineralization in soil, but little is known about the distribution pattern of phosphatase activity in the rhizosphere of *Fagus sylvatica* and the seasonal dynamics of phosphatase activity in soil. We studied the distribution of acid and alkaline phosphatase activity during one year in soils and in the rhizosphere of *F. sylvatica* depending on P availability. For this purpose, we conducted a long-term rhizobox experiment with *F. sylvatica* seedlings and soils of two sites of contrasting P status (Unterluess and Bad Brueckenau). Seedlings and soils were collected at the two sites in February 2014, and transferred to a greenhouse without climate control at the University Bayreuth. The seedlings were planted separately in soil of their original site in large rhizoboxes that were kept inclined in order to make the root grow along the bottom site of the boxes. Half of the rhizoboxes were fertilized with inorganic P (0.1 mg KH_2PO_4-P g^{-1} soil). We determined acid and alkaline phosphatase activity during each season (summer and fall 2014 plus winter and spring 2015) at 20 °C by soil zymography, which is a novel *in situ* method allowing for the analysis of distribution patterns of exoenzyme activity in soil. Additionally, we determined the P contents of the soils and the plants.
The total P content (H_2SO_4-extractable P) in the soils differed strongly between Unterluess and Bad Brueckenau (3 and 583 mg P kg^{-1}, respectively), and the leaf P contents amounted to 0.80 and 1.15 mg g^{-1}, respectively. P fertilization increased the leaf P content, especially in the *F. sylvatica* seedlings from Unterluess, resulting in mean P contents of 1.51 and 1.30 mg g^{-1}, in Unterluess and Bad Brueckenau, respectively.
Acid phosphatase activity was higher in the rhizosphere of *F. sylvatica* seedlings from Unterluess than from Bad Brueckenau at any time of the year (22.83 in Unterluess versus 13.82 pmol mm^{-2} h^{-1} in Bad Brueckenau). The difference in alkaline phosphatase activity in the rhizosphere between the sites was also significant, but less pronounced. While acid phosphatase activity was significantly higher in the rhizosphere at the site Unterluess at any time of the year, acid phosphatase activity in the rhizoboxes of Bad Bruckenau was higher in the soil than in the rhizosphere. This finding indicates that *F. sylvatica* predominantly contributed to the total phosphatase activity in Luess, whereas microbial phosphatase activity seemed to be more important in Bad Brueckenau.
While we found relatively large differences between the two sites and between the rhizosphere and the bulk soil, fertilization did not significantly affect phosphatase activity. This result might suggest that phosphatase activity was not only controlled by P availability but also by other factors such as C availability. Further, we did not observe differences between the seasons of the year except for a decrease in alkaline phosphatase activity in the rhizosphere of the fertilized *F.*

sylvatica seedlings from Bad Brueckenau from summer to fall and fall to winter. The lack of differences between the seasons indicates that phosphatases are produced at very similar rates during all seasons. Yet, their activity in the field might differ from the activities measured here due to different temperature.

In conclusion, this study shows that phosphatase activity differed significantly between the two sites. While *F. sylvatica* contributed strongly to the total phosphatase activity in Luess, microbial phosphatase activity seemed to be more important in Bad Brueckenau. However, we cannot attribute the difference between the sites to the differing P status since P fertilization, which alleviated potential P deficiencies, did not decrease phosphatase activity.

Thursday, July 2

Oral presentation

The challenge of recognizing microorganisms as key players in ecosystem nutrition

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Soil microorganisms have long been known to be central to nutrient cycling in ecosystems. In particular, microbes recycle nutrients from dead organic matter, drive weathering of primary minerals, and improve the nutrition of plants by forming fungal mutualisms with roots and converting atmospheric nitrogen into biologically available forms. The microbial biomass can also constitute an important reservoir of nutrients in the soil, although the relative amount compared to plant remains largely unexplored. In this presentation I will describe two recent examples where soil microbes were found to play a surprising but central role in determining nutrient pools and availability in forested ecosystems. First, I will show how variation in the two predominant mycorrhizal associations between fungi and trees – arbuscular mycorrhizas and ectomycorrhizas – influence soil organic matter stocks in forests worldwide. In boreal, temperate, and tropical latitudes, soils under ectomycorrhizal forests contain 1.7 times more organic carbon than equivalent forests dominated by arbuscular mycorrhizas. This occurs because ectomycorrhizas acquire nitrogen directly from soil organic matter, which reduces decomposition by promoting nitrogen limitation of heterotrophic microbes. Second, I will discuss the quantitative importance of the soil microbial phosphorus in forest ecosystems. Along a retrogressive temperate forest chronosequence in New Zealand, soil microbial biomass contains approximately two times the amount of phosphorus as occurs in vegetation for the majority of the 120,000 year lifespan of the ecosystem. The same phenomenon occurs in a lowland tropical rain forest in Panama, where the microbial biomass contains only 2 % of the biomass carbon, but more than 70 % of the biomass phosphorus. Fifteen years of phosphorus addition has doubled the amount of phosphorus in both the vegetation and the microbial biomass, but the distribution between plants and microbes remains similar to untreated plots. Finally, I will discuss the implications of these findings for our understanding of the role of microbes in ecosystem nutrition, including the response of forests to global change and competition for phosphorus between plants and microbes during long-term ecosystem development.

The relative importance of soil organic phosphorus mineralization in mineral topsoil under beech forest is greatly affected by the availability of inorganic phosphorus

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According to the main hypothesis of the SPP1685, the mineralization of soil organic phosphorus (P) as a P recycling process is more important under low than under high availability of inorganic P. Gross and net organic P mineralization rates in soils can be assessed by an isotopic dilution approach. However, the intense soil disturbance which is commonly applied during labelling of soils with ^{33}P may create artefacts, e.g. through transiently increased microbial activity. To assess the effect of inorganic P availability on organic P mineralization rates (site effect) and to evaluate the effect of soil mixing during labelling (treatment effect), fresh samples from the top horizon of the mineral soil at the beech forest sites in Bad Brückenau (BBR) and Lüss (LUE) were obtained. After homogenization by sieving and pre-incubation at a defined bulk density, soils were labelled with ^{33}P either by injection or by manual mixing. The specific activities ($^{33}P/^{31}P$) in water-extractable and microbial P as well as soil respiration during incubation were then followed over 6 weeks.

One day after labelling by mixing, the soil respiration rate was increased compared to injection in BBR, but this effect was transient and cumulative CO_2-release after 6 weeks was therefore similar in both treatments. In LUE, no significant effect of mixing was observed after one day, but respiration rates tended to be higher after mixing throughout the entire incubation. Cumulative respiration was thus increased by mixing in LUE, but it remained three times lower than in BBR. Water-extractable phosphate was transiently increased by mixing in LUE but not in BBR, presumably due to greater P sorption in BBR. Water-extractable phosphate was initially similar at both sites but showed different temporal trends, increasing in LUE and decreasing in BBR. Specific activities in water-extractable phosphate were not affected by mixing in LUE and variation was similar in both treatments. In contrast, labelling by injection caused highly variable results in BBR. Microbial P was transiently increased by mixing in BBR but consistently reduced in LUE, and it was about 6 times greater in BBR than in LUE. Gross and net organic P mineralization rates could only be calculated for LUE, since physicochemical processes largely dominated soil P dynamics in BBR, preventing the detection of biological processes. In LUE, however, cumulative gross organic P mineralization was 10 times greater than physicochemical P fluxes during the incubation period, and significant net organic P mineralization rates are in accordance with the increase in water-extractable phosphate observed during incubation.

In conclusion, soil labelling by mixing caused transient flush effects but did not cause major artefacts. Soil labelling by injection appears to be feasible for low-P-sorbing soils such as LUE, but not for soils with greater P sorption such as BBR. The relative importance of biological and biochemical processes in soil P dynamics is clearly much more important in the mineral topsoil in LUE than in BBR. In addition, the relative importance of the organic horizons is probably different between the sites, increasing the relative importance of recycling processes in LUE.

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Do microbial carbon use efficiency (CUE) and the mean residence time (MRT) of microbial biomass C depend on soil stoichiometry?

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The ratios of bioavailable elements in soils hardly ever meet the nutritional demands of soil microbial communities. Yet, the microbial biomass stoichiometry is relatively constant. To maintain their biomass stoichiometry, microbial communities can adjust their carbon use efficiency (CUE) and the mean residence time (MRT) of their biomass carbon (C) to the ratios of available elements. Microbial CUE is usually defined as the organic C taken up that is allocated to growth. So far, it is not well understood how microorganisms adjust their CUE and the MRT of their biomass C to ratios of available elements in soils due to a lack of suitable methodological approaches. Microbial CUE has been measured by determining the incorporation and respiration of C from specific ^{13}C-labeled substrates. However, this approach confounds microbial CUE with the specific use efficiency of a given substrate. Moreover, the approach is associated with a large uncertainty since soil microorganisms do not only take up C from the labeled compound that is added, but also from the non-labeled soil organic matter, and they may use both sources at very different rates.

Recently, we developed a method to determine both the microbial CUE and the MRT of the microbial biomass C independently of substrate addition. The new method is based on labeling of microbial genomic DNA with ^{18}O-H_2O. Since genomic DNA is only synthesized when cells are dividing, the incorporation of the ^{18}O-label into genomic DNA can be used to calculate the microbial growth rate. Based on the growth rate and the respiration rate measured concurrently, the microbial CUE is estimated. Moreover, the method can be used to assess the MRT of the microbial biomass C in soil. To calculate microbial MRT, the microbial biomass C is divided by the microbial growth rate.

Here we will show first results on the microbial CUE and the MRT of the microbial biomass C in temperate soil profiles and in grassland soils of a long-term fertilization experiment. The CUE determined based on ^{18}O-labeling was consistently lower than the CUE estimated by ^{13}C labeling. The microbial CUE in organic layers of forest soils was significantly higher than in the mineral soil, where it amounted to about 30 %. In fertilized grassland and cropland soils, the microbial CUE was elevated compared to the mineral horizons of the forest soils. The MRT of the microbial biomass C in the forest soils increased strongly with depth from 8 - 44 days in the organic layer to 253 - 294 days in the B horizon. We will discuss the dependence of the microbial CUE and MRT of the microbial biomass C on (ratios of) bioavailable C, nitrogen and phosphorus concentrations.

Phosphorus depletion in forest soils shapes bacterial communities towards phosphorus recycling systems

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Phosphorus (P) is an important macronutrient for all biota on earth. Many soils throughout the world are deficient in free, plant available P, since the high reactivity leads to precipitation. Microbes play an important role in mineralizing organic and solubilizing precipitated forms of inorganic P, but are also competitors in terms of phosphorus uptake. In this study we investigated the impact of soil P supply on microbial community structures and P cycle associated genes. We analyzed samples from two contrasting beech forest soils containing high (Bad Brueckenau) or low amounts (Luess) of total P. We assume that in a P-depleted soil the recycling of organic bound P is dominant whereas in a P-rich soil the solubilization of inorganic P prevails.

Whole genome shotgun sequencing was carried out using 454 technology. Data analysis was performed implying MEGAN5. Microbial biomass phosphorus as well as microbial carbon and nitrogen contents were determined.

Phylogenetic annotation of datasets (DIAMOND against NCBI Non-redundant database) revealed a domination of *Proteobacteria* (44.9 % of assigned sequences), *Actinobacteria* (21.3 %) and *Acidobacteria* (20.6 %) in both soils. A surprisingly high abundance of *Rhizobiales* was detected in Bad Brueckenau (33.2 %) compared to Luess (16.0 %) ($P<0.0003$). However in Luess *Actinomycetales* (26.8 %) ($P<0.113$) and *Acidobacteriales* (17.2 %) ($P<0.0005$) were among the dominating orders.

Most abundant P cycle associated genes referred to microbial phosphate transporters, including the highly efficient phosphate-specific transporter (Pst) and the phosphate-inorganic transporter (Pit). Both systems showed a higher abundance in the P-depleted soil. Genes involved in P starvation response regulation (PhoB, PhoR) were detected more frequently compared to enzymes performing the mineralization of organic P (e.g. acid and alkaline phosphatases, phytases). This demonstrates the importance of efficient microbial P uptake systems on the one hand and effective gene regulation under P limitation on the other hand, allowing microbes to succeed in the struggle for phosphorus with plants. Regarding inorganic P solubilization, a significantly higher microbial potential was detected in the P-rich soil. This trait especially referred to *Candidatus* Solibacter usiatus, likewise one of the dominating species in the datasets. Moreover, predicted enzymes were primarily harbored by *Rhizobiales*, *Actinomycetales* and *Acidobacteriales*. Interestingly *Rhizobiales* contributes to soil P cycling predominantly in Bad Brueckenau, whereas in Luess a stronger involvement of *Actinomycetales* and *Acidobacteriales* was detected. This also reflects the total abundance of microbial orders in the two different soils. Direct targeting of the functional microbial community uncovered the hitherto unseen contribution of certain taxa to soil P cycling. Our results further corroborate the hypothesis that in a P-rich soil the solubilization of inorganic P plays a major role. However a higher potential for efficient microbial phosphorus uptake systems was detected in the P-depleted soil.

Composite plants: a versatile tool for promotor analysis in ectomycorrhizal symbiosis.

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Ectomycorrhiza formation, the result of a symbiotic interaction of fine roots of woody plants and certain soil fungi, leads to a better nutrition of the plant partner. For the requested bidirectional nutrient and metabolite exchange, plant and fungal metabolisms have to be adapted. To address control mechanisms of ectomycorrhizal association, we want to identify regulatory elements controlling plant gene expression in symbiosis.

A prerequisite for such investigations is the formation of transgenic plants. For poplar (*Populus tremula x alba*), a plant model frequently used in ectomycorrhizal research, the generation of conventional transformants lasts for about one year. So called composite plants, where the formation of transgenic roots is induced by the inoculation of stem sections by *Agrobacterium rhizogenes* infection, could accelerate such an approach. We have thus developed a protocol that allows the formation of ectomycorrhizas on transgenic roots of poplar composite plants within a time frame of about 6 month. Six different *A. rhizogenes* strains were analyzed for their ability to form composite poplar plants harboring transgenic roots. Finally, one *A. rhizogenes* strain was chosen because of the simplicity of its transformation procedure and its robust capability to induce transgenic root formation. A problem observed by *A. rhizogenes* induced root formation is that transgenic roots frequently reveal a modulated phytohormone perception, visible by a "hairy root" phenotype. Elevated hair formation and modulated graviperception was also observed in roots of composite *Populus tremula x alba* plants. As phytohormones are discussed to be involved in ectomycorrhizal symbiosis, we had to proof the capability of composite plants in mycorrhiza formation. However, ectomycorrhizas were obtained from transgenic roots of composite plants in a similar frequency as from roots of control plants. Furthermore, both ectomycorrhizal structure and the expression of marker genes did not differ between roots of composite plants and those of non transgenic controls. One of challenges that we faced with poplar ectomycorrhizas was the strong autofluorescense of infected fine roots, which hamper the application of fluorescent proteins. We will present strategies to overcome this problem, making composite plants to a versatile tool in ectomycorrhizal research.

Phosphorus mobilization from forest soils by ectomycorrhizal fungi: recent data and actual role

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It is assumed that the most important role of (ecto)mycorrhizal symbiosis is to improve the P nutrition of the host-plant. Several hypothesis have been proposed to explain this positive role of the symbiosis that are (1) the increase of soil exploitation and P uptake by the fungus developing outside the roots, (2) the capacity to produce organic anions to mobilise adsorbed mineral P and (3) the capacity to produce enzymes, especially acid phosphatises able to mineralize organic P forms, to release free inorganic P (Pi) that could benefit to the host plant. The talk will present the results we obtained regarding the possible role of ectomycorrhizal symbiosis to mobilize soil mineral and organic P from forest soils. We worked mainly with *Pinus pinaster* as a model species. We used different approaches either in the field or in the laboratory. In the field, we explored the diversity of the ectomycorrhizal species associated with 14 year-old *P. pinaster* plantations as a function of fertilization (no fertilization, P or NPK fertilization) and irrigation. We also measured the enzyme activities produced by the ectomycorrhizal tips to assess their variability as a function of the fertilization treatment and/or the fungal species. In the laboratory, we cultivated young seedlings in rhizoboxes containing soil collected either near Montpellier (chromic cambisol) or from the same *P. pinaster* plantation, mentioned above. We cultivated young *P. pinaster* seedlings, whether or not associated with “laboratory” fungal species such as *Rhizopogon roseolus* (strong oxalate producer) or *Hebeloma cylindrosporum* (strong acid phosphatase producer), or with native fungal species from field soil samples. We studied also the interactions between ECM plants and other actors of the P cycle that are bacteria able to mineralize phytate, a recalcitrant organic P source, and their predators that are bacteria-feeding nematodes.

In the field, we detected ≈ 20 species using DNA extracted from individual ECM tips and ITS sequencing. As expected, the fertilization regime modified the diversity of the ECM species associated with the roots with the maximum level of diversity found in irrigated, not fertilized plots (18 species) and the lowest one in non irrigated, fully fertilized plots (5 species). We found that N-acetlyl-glucosaminidase (NAG) and acid phosphatase (AcPAse) activities were the highest ones among the 8 activities assayed. Contrary to the NAG that did not vary much between treatments, the AcPAse could vary with fertilization but the variations seemed to depend first on the species. In the laboratory experiments, if our results demonstrated the importance of the fungal oxalate release to mobilize mineral P towards the host plant, our results are more in favor of an indirect role of the ectomycorrhizal fungi to mobilize organic P present in the medium. Therefore a new model of ectomycorrhizal functioning will be proposed.

Ectomycorrhizal communities in relation to a phosphorus gradient

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The concentration of phosphorus (P) in soil solutions is generally low. Furthermore, the total stocks of inorganic and organic P vary between different ecosystems. Forests in Central Europe are usually not fertilized. Therefore, trees in these ecosystems, which may live for centuries, must have developed adaptation strategies to cope with differences in P availability. Most tree species in temperate European forests, including the dominant species beech (*Fagus sylvatica*) form mutualistic associations with ectomycorrhizal fungi (EMF) at their root tips. EMF form a novel organ with the root tip, the ectomycorrhiza (EM), which is known to improve the P supply to the host tree. In different environments, beech encounter different nutritional situations. We hypothesized that the EM community composition associated with the roots differed between beech forests differing in P availability. We further hypothesized that ecosystems in which P was mainly recycled from organic matter were dominated by EMF with saprophytic properties leading to high soil phosphatase activities; whereas forests, in which inorganic P must be accessed, were dominated by EMF known to produce organic acids. To address these hypotheses the EMF community structures were studied at five research sites in Germany including: Bad Brückenau, Conventwald, Mitterfels, Vessertal and Luess. The sites represent a gradient of decreasing supply of mineral P. We characterized P availability, root P concentrations, microbial biomass, phosphatase activities and root EMF composition. We found strong differences in soil P concentrations and increasing EMF diversity at P rich sites. The P concentration of fine roots was almost unaffected by the edaphic conditions across different ecosystems suggesting that the community shifts in EMF contributed to counterbalance differences in environmental P availability for roots.

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A novel ^{33}P labelling approach: Competition between roots and microorganisms for phosphorus

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Our knowledge about the seasonal variation of microbial phosphorus uptake is limited compared to other key nutrient elements. An initial hypothesis suggested that the dynamics of P uptake and mineralization by microorganisms in temperate forest soils exhibit a seasonality anti-cyclic to plant P uptake. Therefore, the ratio of microbial P to labile P increases by the transition from acquiring ecosystems (in spring) to recycling ones (in fall).
To investigate this, intact soil-plant mesocosms containing Ah horizon with 1 year old *F. sylvatica* were removed from the P-rich field site Bad Brueckenau and the P-depleted field site Luess in Germany. During incubation under controlled conditions, seasonal pulse labeling by ^{33}P-orthophosphate was performed at 5 time points over the course of one year. ^{33}P recovery in microbial compounds of organic and mineral soil horizons was determined 7 and 30 days after the labeling. This procedure accounts for temporal changes in P allocation and also considers the rather slow P transport from the mycorrhiza into the plants and other microorganisms. For the first time we analyzed the ^{33}P incorporation into total PLFA and consequently provide a new technique for the analysis of P uptake by microorganisms, which has clear advantages compared to P quantification after chloroform fumigation.
Microbial P incorporation exhibited a distinct peak during the summer months, coinciding with the seasonally largest amount of microbial biomass in the soil. Only small differences between spring and fall were found. A concurrent development was seen in the ^{33}P uptake rate per day, where spring and fall showed a very similar pattern of a slow, continuous incorporation. In contrast, during summer the ^{33}P uptake was nearly completed after seven days. This was especially evident in the soil from the P-depleted Luess field site. The microbial P uptake of the organic upper soil layer exceeded that of the mineral soil by a factor of 10 to 20 at both field sites. This points to the soil C content and consequently the amount of microbial biomass as the determining factor for the microbial P uptake. In contrast, seasonal plant P uptake pattern seem to play a minor role suggesting a higher competitiveness of soil microorganisms for phosphorus than plants.

Do interannual variations of phosphorus contents in tree rings of norway spruce *(Picea Abies)* and scots pine (*Pinus Sylvestris)* reflect temporal variations in phosphorus availability?

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Many European forests have become phosphorus (P) limited in recent decades, possibly due to increased nitrogen deposition, soil acidification and improved tree growth. Dendrochemical analyses of P might enable a retrospective analysis of P nutrition of trees and provide valuable information about the effect of short-term changes as well as long-term environmental trends on P availability in forest ecosystems. However, this approach requires clear signals in P content in year rings that is not blurred through retranslocation processes between year rings.
Therefore, we compared tree ring P contents in heartwood of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) from 2 fertilization trials in Southern Germany. Using a before-after control-impact design we sampled year rings from fertilized and unfertilized plots in wood formed before and after P fertilization. We analyzed stem discs from 5-6 (co-) dominant trees per plot at 1.3 m stem height. Phosphorus contents were determined for individual year rings for the 5 years prior to fertilization, the year of fertilization, and 15 years after the fertilization event. Annual sections of wood strips were shaved off, ground and digested in HNO_3 under pressure prior to ICP-MS analysis.
The application of 70 kg P ha^{-1} resulted in a prompt and extended increase in wood P contents at both sites. The fertilization signal remained clearly visible until the end of the 15-year observation period. Before P fertilizer application, P contents in year rings varied considerably between individual trees. Hence, the response to P fertilization of trees with very low P contents prior to fertilization was more pronounced than that of trees with higher initial wood P contents. Importantly, there was no evidence for a translocation of fertilizer P into year rings that were formed prior to fertilization.
Our findings suggest that P content in year rings of Scots pine and Norway spruce heartwood may be a suitable indicator for changes of P availability in forest ecosystems.

Phosphorus acquisition, storage, and mobilization in beech and poplar trees during annual growth

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Phosphorus is one of five macronutrients essential for plant growth and development. Because of its low availability in many forest soils, efficient uptake, use and cycling in plants and ecosystems are required. Furthermore, these processes have to be adapted to changing phosphorus demands throughout the annual growth cycle. It is commonly accepted that P acquisition occurs by the uptake of inorganic phosphorus sources (P_i) from soil water or from organic bound phosphate after cleavage by phosphatases. Whether also organic P sources (P_{org}) are taken up by the roots is currently unknown. Phosphorus acquisition from inorganic P_i (Km, v_{max}, pH and concentration dependency) and organic P (P_{org}) (i.e. ATP, glucose-6-phosphate, NADPH) by poplar and beech roots were characterized under controlled conditions and also analysed in the field. P acquisition of beech trees differs not only for P_i and P_{org}, but also with the availability of P_i from the soil (low and high P soils) and during the seasons. It is assumed that the latter difference is due to different P requirements during the annual growth cycle, but also to avoid competition between young and adult trees.

Phosphorus cycling within trees during the annual growth cycle is needed to allow spring growth of new leaves. Seasonal P cycling includes P storage in bark and wood tissues during autumn and winter as well as mobilization from these tissues during spring. In order to obtain a first insight into tree internal P cycling, phosphate levels were determined in leaves (buds), bark and wood as well as in xylem saps and phloem exudates. Beech trees from two core sites of the SPP 1685 that differ in P availability, i.e. a field side with high (Conventwald, acidic soil) and a field site with low soil contents (Tuttlingen, calcareous soil) of easily available P were investigated. The results show differences in P nutrition of these forest ecosystems that are to be expected for a P acquiring and a P recycling ecosystem. Field grown poplars were included in these investigations as a tree species that allows molecular analyses of the processes investigated and for species comparison.

Effects acidification by nitrogen input and liming on the P_{ortho} concentrations in the soil solution

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Introduction: Though phosphorus (P) is one of the most important nutrients, its cycle in forest ecosystems is poorly understood, especially the effects of two human induced influences namely acidification by nitrogen input and liming. Even P_{orhto} in the soil solution is only a small part of the total P in the soil, it is the transition form from one P pool to another, is easily available for plants and other organisms and is susceptible to leaching.
To quantify the impact of factors controlling the P_{ortho} concentrations in the soil solution we conducted a meso-cosm experiment.
Method: 128 undisturbed soil cores were taken from 3 sites along a gradient of decreasing supply of easily available P (Bad Brückenau -rich, Vessertal - meso, Lüss -poor) each containing the two subsites beech and spruce. Each soil core had a diameter of 7.4 cm and contained 20 cm mineral soil plus the organic layer (ranging from 1 to 9 cm). The soil cores were irrigated with artificial rain (AR, control), AR plus a NH_4NO_3 addition (acid) or AR plus a $CaCO_3/MgCO_3$ addition (lime). Soil solution was collected at 3 depths in each soil core: below the organic layer (top), at the middle of the mineral soil (middle) and at the bottom of the cylinder (bottom). The suction cups consist of boro silicate with a porosity of 10 to 16 µm. The applied vacuum ranged from 10 to 50 hPa. After an adaption phase of 102 days, soil solution was collected 3 times as collective sample for a periods of 74, 70 and 84 days. P_{ortho} was determinded with the molybdane blue method. The results were analyzed with a Kruskal Wallis Test at a 5% error probability.
Results: We could show that the acidification by means of NH_4NO_3 let to a significant increase of P_{ortho} in the top and middle parts of the soil cores at the poor beech site as well as at the top and bottom of the meso beech site. At the poor and meso spruce sites an increase could only be observed at the bottom part. The rich sites (beech and spruce) did not show any response to the treatment.
Liming let to a reduction of P_{ortho} only at two locations, the poor beech site at the middle part and in the top part of the poor spruce site.
Discussion: Acidification did lead to an increase of P_{ortho} in some parts of the poor and meso sites. We assume two mechanisms let to this effect. First: The acidification let to an increased solution of apatites (a significant increase of Ca in solution supports this assumption). Second: the decrease of pH on already acid soils restrained organisms thus impeding an uptake of P_{ortho} an effect that did presumably not occur on the rich site where the pH remained above the critical level of 4.2.
Liming had a negative effect on P_{ortho} in just two cases, we assume through the formation of apatites. We hypothesis the total input of CaCO3/MgCO3 within the experiment time was not sufficient to cause stronger effects.

Perspectives of microdialysis for analysis of phosphate availability in soils

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Microdialysis is an established method in pharmacokinetics that allows sampling of dissolved compounds by diffusive flux in a sub-millimeter environment. Simultaneously it is possible to release substances from the perfusate by retrodiffusion into that environment. Both characteristics in combination with a minimized mechanical and chemical impact make microdialysis a promising tool to simulate rhizosphere processes. However, until now most available micrcodialysis studies in soils focused on nitrogen and no data is available for phosphate. We used commercially available Polyarylethersulfone Microdialysis probes with a 520 μm diameter and a 4 mm effective membrane length. Perfusate was moved with push-pull technique by a peristaltic pump with flow rates between 0.4 and 20 μl/min. When tested in bulk solution, recovery of phosphate decreased with flow rate and increased with ionic strength of the external solution. Phosphate recovery was lower than that of nitrate and chloride, but higher than that of sulphate. In actual soil samples phosphate could be recovered in measurable concentrations only through retrodiffusion of citric acid from the perfusate. The effects of diffusion, adsorption and depletion around the probes has been simulated with a finite-difference model. Modelling results were in good agreement with observations. Diffusive exchange around the microdialysis membrane depletes its direct (sub-mm) environment and subsequent diffusive supply is extremely low due to strong adsorption. Depletion radius and recovery is strongly increased by citrate retrodiffusion which changes the adsorptions characteristics. As our first results show microdialysis is a suitable technique to simulate some important features of soil-root transfer of phosphorus. However, small sampling volumes of dialysate and phosphate concentrations in the sub μg/l range are a challenging analytical task.

Small Aggregates as temporary storage of P in forest soils?

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Phosphorus availability for plants depends on small scale heterogeneity in soils. Till now only little is known about the role of soil aggregates for the P availability in forest soils. The aim of our study is to (1) link the properties of soil aggregates (< 2 mm) to the P distribution within aggregates, and (2) to get insights into seasonal dynamics of aggregates.
Soil samples from five study sites across Germany were investigated. These study sites follow a sequence of decreasing availability of mineral-bound P. We use the following methods to describe the properties of aggregates:
The content of P_{PO4} from in citric acid extracts was determined from soil samples with undisturbed aggregates and soil samples homogenized by ultrasound. Density fractionation combined with ultrasonic treatment was used to separate three fractions of organic carbon from the soil aggregates (free light fraction, light fraction occluded in aggregates and heavy fraction associated tightly to mineral surfaces). The P content of the three fractions was analysed in ignited samples by sulfuric acid extracts and UV/VIS spectroscopy. Density fractionation of soil organic matter was conducted with soil samples taken in spring, summer and winter, respectively.
Disaggregation of soil samples increased solubility of P_{PO4} by up to 21 %. The concentration of P associated to occluded particulate organic matter ranged from 2 mg to 41 mg kg^{-1} soil. The analysis on the seasonal dynamics of organic matter indicates the integration of free light fraction into aggregates and onto mineral surfaces from spring to autumn and winter. We conclude that aggregates represent a temporary P sink, which may be mobilized following aggregate disruption.

Investigating spatial patterns of phosphorus speciation in soil aggregates by combining NanoSIMS, µXRF and µXANES

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In recent years it has become apparent that nano- and micro-structures in soil aggregates highly determine the availability and allocation of phosphorus (P) in soil. Apart from wet-chemical methods, nowadays increasingly advanced technologies are available to identify and quantify P in various binding forms. In contrast to wet-chemical procedures, the following advanced technologies allow studying the small-scale spatial distribution of different P species in soil aggregates: nano-scale secondary ion mass spectrometry (*NanoSIMS*), and spatially resolved X-ray absorption spectroscopy (*µXRF*; *µXANES*).
Thus, *NanoSIMS* enables to determine the distribution of up to seven ions on the surface of a thin-sectioned soil aggregate with spatial resolution of about 100 nm. *µXRF* also allows for elemental mapping, but with larger spatial resolution (0.5-1µm), greater penetration depth, and only for elements that show fluorescence up to a specific energy. Through analysis of the co-localization of particular elements/ions it is possible to assess the P binding form at different micro-spots indirectly. Spectra of *µXANES* measurements on, *e.g.*, P *hot spots* finally allow a direct quantification of different P species, by linearly fitting the respective spectra with combined shares of P standard reference spectra. Combination of all three methods is a powerful approach to investigate spatial patterns of P speciation in soil micro-structures.
We present data from four soil aggregates collected in two German forest soils with different ecosystem P status (near *Unterlüß* and *Bad Brückenau*, respectively), and from two different soil depths. The methods used for aggregate preparation and P speciation analysis are discussed, as well as first results from all used techniques. Additionally we discuss the advantages and drawbacks of the applied methods for the assessment of spatial heterogeneity of P speciation in soil aggregates.

Friday, July 3

Oral presentation

Long-term and large-scale macronutrient modelling in terrestrial ecosystems

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The last two centuries have seen widespread anthropogenic nutrient pollution and land use disturbance in Europe. Tools are needed to explore the resultant changes in soil stores of C, N and P, fluxes of these nutrients to air and water, and plant system response. Such a model would need to integrate C, N and P cycles and be capable of simulating large areas (regional scales) over long timescales in accordance with the process timescales and the centuries of anthropogenic forcings.

A new model of C-N-P plant-soil interactions, N14CP, is introduced which is applicable to natural and semi-natural ecosystems over long timsescales and regional spatial scales, and is designed to run with widely available input data (climate, vegetation history, atmospheric deposition) and with simple assumptions about mineral weathering. The model integrates the C, N and P cycles of topsoil through mineral weathering of P and base cations, N fixation, organic matter decomposition, N and P immobilisation in organic matter, P sorption, denitrification, leaching, and nutrient uptake by plants. Plant growth may in principle be limited by temperature or rainfall, but in practice it is by nutrient availability. Plant biomass is formed according to the available N and P, constrained by the plant element stoichiometry. Plant litter returned to the soil then drives soil organic matter cycling. Subsoil element pools form by the downward leaching and retention of dissolved organic matter. N14CP is run from the start of the Holocene (no soil) so that the soil element pools build up under essentially natural conditions until 1800. Then anthropogenic factors begin to exert their influences. We parameterized and tested N14CP against site data from across northern Europe, providing the most robust test of such a model to date.

Comparison against field observations demonstrated that N14CP can represent broad trends in nutrient change across multiple soil nutrient pools and fluxes. However, inter-site variation was not well reproduced. Weatherable P emerged as an important control on ecosystem development and on contemporary pools and fluxes of carbon, nitrogen and phosphorus. By allowing the weatherable P pool at each site to vary within reasonable boundaries, explanation of inter-site variation was considerably improved. We calculate that nitrogen enrichment from atmospheric deposition has increased net primary productivity, the soil storage of C and N, and the leaching of inorganic nitrogen and dissolved organic matter.

N14CP is component of an integrated model being developed in the LTLS project (www.ltls.org.uk), with the aim of simulating changes in macronutrient pools and fluxes in all UK semi-natural and agricultural terrestrial ecosystems and freshwaters, over the last 200 years.

Phosphorus in Forest Stream Waters – The Relevance of Nanoparticles and Colloids

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Headwater catchments within undisturbed forest ecosystems reflect the natural load of nutrients and minerals cycled or released from the ecosystem; yet, little is known about the role of natural nanoparticles (1 - 100 nm) and fine colloids (>100 nm - 450 nm) as stream water nutrient carriers. It is hypothesized that relevant amounts of P, Fe, Al, Mn, Si and organic C in stream waters occur in nanoparticulate and fine colloidal forms, but with variations in size, chemistry and proportions in the fractions. Field Flow Fractionation (FFF) coupled to an Inductively Coupled Plasma Mass Spectrometer (ICP-MS) and an Organic Carbon Detector (OCD) provided a size resolved assessment of nanoparticles and fine colloids below 0.45 µm. Natural nanoparticles and fine colloids could be assigned to three main fractions (1 kDa - 20 nm, >20 nm - 60 nm, >60 nm - 300 nm). Despite a considerable variation between the streams, cluster analysis of the fractionation results revealed that each fraction comprised unique elemental signatures with different preferential P binding partners. With increasing size, the preferential binding of P to Fe shifted to organic C and in the largest size fraction to clay minerals. The proportions of P bound to nanoparticles and fine colloids increased with increasing C:P ratio and decreasing truly dissolved P content along the streams. Hence, natural nanoparticles and fine colloids play a central role in riverine P cycling and export and these fractions gain importance as the overall P status of the catchment declines.

Isotope geochemical determination of phosphorus weathering sources and fluxes in forest ecosystems

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Nutrients, such as Phosphorus (P), are released by chemical weathering and therefore become bioavailable. This study serves to estimate the rate at which P is released at two study sites in the Black Forest and the Bavarian Forest and to fingerprint the source and depth at which plants assimilate P. Therefore, innovative geochemical tools like meteoric and in-situ produced ^{10}Be, and traditional source tracer like radiogenic strontium isotopes are applied.

In order to determine the depth and source at which plants take up Phosphorus 20 - 30 m deep drilling cores at the hill slope in the Black Forest and the Bavarian Forest were sunk. Both boreholes were constructed to groundwater monitoring wells. Additionally, a well at the ridge top in the Black Forest has been sunk in order to check for spatial heterogeneity and to avoid periglacial cover beds (e.g. Schaller *et al.*, 2002). Moreover, surficial regolith has been sampled at depth intervals of 20 cm. Regolith and bedrock samples were analyzed for bulk elemental composition with XRF and ICP-OES, mineralogically with XRD and isotopically for bulk and sequentially leached extracts for ^{87}Sr/^{86}Sr and ^{10}Be/^{9}Be.

Phosphorus release fluxes will be determined by concentration measurements of in-situ produced ^{10}Be of bedload sediment and topsoil. Therefore, chemical depletion fractions (Riebe *et al.*, 2003) and the mass transfer coefficient of P (τ_P) are applied.

Furthermore, bulk elemental composition and ^{87}Sr/^{86}Sr of plant tissues like needles, sapwood and heartwood as well as stream water and bedload sediment at both study sites have been sampled and measured.

In cooperation with geophysicists three seismological depth profiles in parallel to the hill slope in the Black Forest have been measured. Since one of the profiles is connected to the drilling core a direct calibration of P-wave velocity patterns to the geological conditions is possible. The aim of this investigation is to identify the thickness of the regolith spatially.

Based on mass transfer coefficients and radiogenic strontium isotopes our first and preliminary findings indicate that the Black Forest displays a recycling ecosystem while the Bavarian Forest tends to represent an acquiring ecosystem.

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Is lateral subsurface flow the missing sink of P in mountainous forest ecosystems?

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Lateral subsurface flow is the dominant runoff generation processes in many mountainous forest ecosystems, in particular in areas with low permeable bedrock or periglacial covers. Lateral flow in forests is generated in different depths, but preferential flow or flow in the organic layer is most common. Most studies on nutrient export, in particular P, are focusing on vertical flow pathways, but lateral flow in larger pore systems may be a significant export pathway of P. Using a combination of models and novel observations in the field, we analyze the dynamic and export of P in lateral subsurface flow and we will discuss possible explanation of the relevance of these flow pathways.

Dissolved organic phosphorus (DOP) and its potential role for ecosystem nutrition

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During ecosystem development and soil formation, primary mineral sources of phosphorus are becoming increasingly depleted. Inorganic phosphorus forms tend to be bound strongly to or within secondary minerals, thus, are hardly available to plants and are not leached from soil. What about organic forms of phosphorus? Since rarely studied, little is known about the fluxes of dissolved organic phosphorus (DOP) forms and their role in the P cycle. However, there is evidence that DOP is composed of some plant-derived organic phosphorus compounds, such as phytate, which are less mobile and prone to be sorbed to mineral surfaces, whereas microbial-derived compounds like nucleic acids and simple phospho-monoester may represent more mobile forms of soil phosphorus. In our study, we estimated fluxes, composition, and bioavailability of DOP along a gradient in phosphorus availability at five sites on silicate bedrock across Germany (Bad Brückenau, Conventwald, Vessertal, Mitterfels and Lüss) and at a calcareous site in Switzerland (Schänis). Soil solution was collected at 0 down to 60 to 150 cm soil depth at different intervals. Since most solutions had very low P concentrations (<0.05 mg total dissolved P/L), soil solutions had to be concentrated by freeze-drying for the enzymatic characterization of DOP. In order to test the potential bioavailability, we used an enzyme assay distinguishing between phytate-like P (phytate), diester-like P (nucleic acids), monoester-like P (glucose-6-phosphate), and pyrophosphate of bulk molybdate unreactive phosphorus (MUP). First results from the enzymatic assay indicated that monoester-like P and diester-like P were the most prominent form of the hydrolysable DOP constituents. Phytate-like P was almost only present in soil solution from the organic layer and top soil. In leachates from the organic layer, there was a high enzymatic activity for monoester-like P, indicating high recycling efficiency and rapid hydrolysis of labile DOP constituents. DOP was the dominating P form in soil solution at some of the sites, with a greater contribution to total dissolved P in winter than in summer. Concentrations of DOP decreased along the phosphorus availability gradient from less to the more developed forest ecosystems.

Dissolved organic phosphorus (DOP) and its potential role for ecosystem nutrition

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Nitrogen cycling in forest ecosystems in a changing climate

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Many tree species have developed in evolution on marginal soils with low nutrient availability Therefore, trees are thought to be highly adapted to multiple nutrient limitations, in particular of nitrogen and phosphorus, and to possess a low nutrient demand for growth and development. The later was found not to be correct for temperate forest species such as spruce or beech that require more than 100 kg N ha^{-1} a^{-1} in mature forests and, thus, have a similar nitrogen demand as reported for many agricultural systems. Apparently, high N demand at low N availability in temperate forest trees is rather met by long-term ecosystem N accumulation in a largely closed ecosystem N cycle. Since water relations and nutrient acquisition of trees are known to strongly interact with each other, it may be assumed that changes in precipitation and precipitation distribution, as projected from global climate change at the regional level, have the potential to impair processes within the closed ecosystem N cycle of temperate forest and, hence, tree N nutrition. This is of particular significance for beech, the potential natural vegetation in large areas of Central Europe. This tree species is considered highly sensitive to drought, but is highly abundant all over Europe in ecosystems on calcareous soils with low N availability and low water storage capacity. Recent projections on future distribution of beech estimate that this tree species may be largely extinguished on calcareous soils until 2080 as a consequence of global climate change. We hypothesize that this may not only be due to the fragile water relations of beech, but also to disturbance of processes in ecosystem N cycling. In this lecture experimental approaches with beech trees under greenhouse conditions and in the field will be reported that were aimed to test this hypothesis. These approaches include exposure of young beech to labeled litter, girdling of young and mature trees, as well as exchange of monoliths with young beech trees between cool moist and warm dry forests. The results of these studies clearly show that processes at the beech tree and the microbial community level as well as the competitive interaction of beech trees and microbial communities for N are strongly affected by drought and mediate severe changes in ecosystem N cycling.

Land-use impact on phosphorus fractions in tropical soil in Sumatra Indonesia

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Phosphorus (P) is one of the most essential nutrient elements that often limit plant productivity especially in most humid tropical regions like Indonesia. In Sumatra Indonesia conversion of native forest to agricultural land use is relatively increasing over the past several decades. Nonetheless, the effect of land-use change on the chemical forms of soil phosphorus remains unclear. Using a space-for-time substitution (paired-area) approach, we collected and examined soil samples from forest (F), jungle rubber (JR), oil palm plantation (OP) and rubber tree plantation (RT) of comparable geology, parent material and soil type. To assess the different P fractions and P availability the Hedley sequential fractionation scheme was used. The surface layer in all soils showed the highest P concentrations in all analyzed P fractions. Total P in surface horizons ranged between 105 and 175 mg P kg^{-1}, being lowest on soil from OP and highest from F. More chemically stable Po and relatively insoluble Pi forms (residual P) occurred about 41 to 62 % of the total P. Labile phosphate which includes water-extractable P and inorganic (Pi) and organic (Po) P extracted in 0.5 M $NaHCO_3$, occurred in small concentrations (13.90-25.54 mg P kg^{-1}) being highest in F and only accounted for between 11.08 % to 15.05 % of the total soil P in the surface layer and much more lower in the subsurface layer. Although in this study, we include water-extractable P and not the anion-exchange extracted P to calculate for the labile P. Moreover, conversion of forest to oil palm and rubber tree plantation significantly reduces labile P for almost 50% of the labile P in forest. Microbial biomass phosphorus (MBP) also occurred in small concentrations in all soils accounted only between 1.44 to 6.67 % of the total soil P and no significant differences was found in all soils. Furthermore, Pearson's correlation analysis of soil carbon content to labile P, MBP, $NaHCO_3$ Po and total Po was found significant ($P<0.0001$). This suggests that soil organic matter is important in maintaining P availability. We concluded that conversion of forest to plantations influenced the distribution of the different forms of P.

Phosphorus P nutrition types of forest ecosystems: First results on functioning and diagnostic properties

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The overall hypotheses of the priority programme 1685 "Ecosystem nutrition" is that **the P depletion in soils along time drives the evolution of forest ecosystems from P-acquiring systems depending on processes, which mobilise P from the mineral phase to P-recycling systems with high recycling efficiency** (see Figure 1). This development promotes uncoupling of plant nutrition from the mineral soil and the formation of the forest floor. Accordingly, we expect that P acquiring systems have established at sites with low contents of P in the mineral soil, while P recycling systems occur at sites poor in P in the mineral soil. The presentation aims at opening the discussion regarding this hypothesis. Results of the partners of SPP 1685 indicating different kinds and intensity of P acquiring and recycling processes along a geogenic P gradient will be summarized. Diagnostic properties of the proposed nutrition types are introduced which might enable the regionalisation of different types of forest P nutrition.

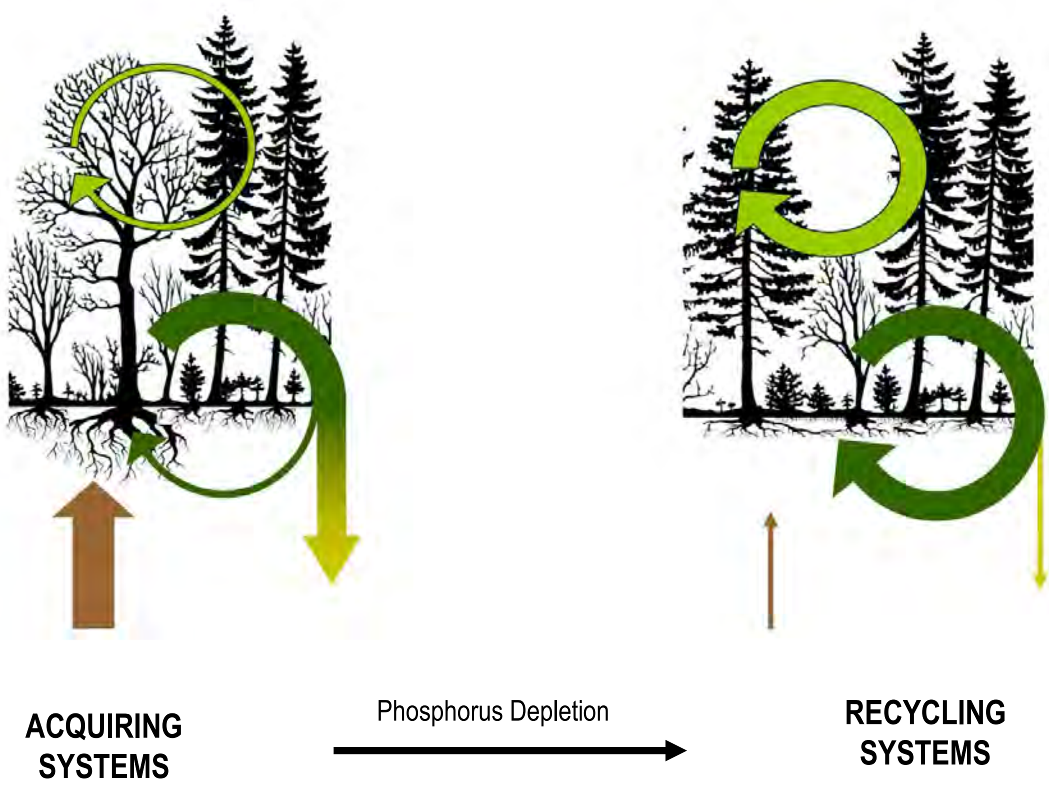

Figure 1: Graphical abstract of our hypothesis on P nutrition of forest ecosystems and the shift from acquiring systems to recycling systems.

Poster

Wednesday, July 1 & Friday, July 3

The importance of fungal-fungal and bacterial-fungal interactions for phosphorus dynamics in forest soils

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Plant uptake of phosphate (P) in complex forest ecosystems relies to a great extent on microbial mineralization of P from organic and inorganic sources, but the relative contributions of the microbial communities to P cycling and allocation in forest soils is not yet very well understood. Multiple interactions within the soil community could stimulate or reduce the P available for plant growth. In this connection the fungal-fungal and bacterial-fungal interactions play a decisive role.

We anticipate that: (I) organically bound P substrates do promote antagonistic effects between saprotrophic fungi (SP) and ectomycorrhizae (EM) due to strong competition. (II) Inorganically derived P compounds benefit synergistic effects between fungi and bacteria due to a bacterial mobilization of P-substrates. Structural differences between the fungal and bacterial community compositions could thereby result from an accumulation of associative bacteria within the mycosphere.

To proof our hypothesis we performed a systematic exclusion of EM-hyphae in the field at five beech-wood forest sites by the use of a meshtube trenching experiment. It is hypothesized that the selected sites (BBR, CON, VES, MIT and LUE) form a gradual shift in allocating P from recycling systems (BBR) to acquiring systems (LUE). We installed eight meshtubes in spring 2014 (four "open" and four "closed" tubes) into the upper soils in the distance of 2.5 m to five *Fagus sylvatica* L. individuals respectively. The tubes ensure selective fungal hyphae ingrowth. "Open" tubes are surrounded by a 50 µm mesh-window to permit access to EM- hyphae. "Closed" tubes prevent for lateral fungal ingrowth. Both tubes comprise the native fungal SP community. The tubes were exposed for a period of 15 months. After 3, 6, 12 and 15 months, five tubes of each treatment are removed with five additional undisturbed soil samples.

Tube derived soils and control samples were analyzed for: (1) microbial bound P contents (P_{mic}), (2) potential phosphatase activities (PAs) and (3) microbial community composition (PLFAs). First results after 3 months and 6 months showed that the sites differ in their potential to mineralize organic P compounds and in their microbial community composition. We found differing water soluble P fractions (ranging from 84.5 to 2.0 mg kg^{-1}) and differing P_{mic} fractions (ranging from 29.0 to 3.1 mg kg^{-1}). Differences in potential phosphatase activities were found ranging from 130.8 to 8.0 µg *p*-nitrophenol $g^{-1}h^{-1}$. PLFAs of $Gram^{+}$ and $Gram^{-}$ bacteria showing small differences between the sites and sampling dates ranging from 87.9 to 15.0 nmol g^{-1} (G^{+} bacteria) and 23.9 to 4.4 nmol g^{-1} (G^{-} bacteria). The fungal PLFA marker (18:2ω6,9) followed a gradual shift from BBR to LUE ranging from 7.7 (BBR) to 2.1 (LUE) nmol g^{-1} indicating higher fungal abundances in the open tubes compared to the closed variants. Therefore, a successfully systematic EM exclusion can be supposed. A further validation by molecular analyses (qPCR, pyrosequencing) is planned as next steps in collaboration with A. Polle (Uni Göttingen).

The isotope signature of subsoil P – evidence of different bioaccessibility?

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Plants may take up between 10 and 80% of their P demand from subsoils, but the forms, accessibility and particularly the residence time of subsoil P in forests are currently hardly understood. Here we aimed at testing the hypothesis that at increased P deficiency in the surface soil there is an increased utilization of subsoil P. As a first step for testing this hypothesis, we quantified (i) the organic and inorganic P stocks in different subsoil compartments of the central field sites, (ii) elucidated changes in organic P bonding forms by means of ^{31}P-NMR spectroscopy, and (iii) characterized the accessibility of the Hedley HCl-extractable subsoil P on the basis of its $\delta^{18}O$ signature. For the latter we optimized the pretreatments in Hedley fractionation and method protocols published by Tamburini et al., (2010; EJSS).
The results indicated that the sites differed in their subsoil P properties, therewith offering different pathways to cope with P deficiency in the surface soil. At sites MItterfels, Vessertal and Luess, the portions of monoester P increased with depth in dialized EDTA/NaOH soil extracts. The Conventwald, in turn, showed an increase in diester P with depth. Overall, the ratio of monester-to-diester P was quite variable, ranging from 1.9 to 13.
The assessment of $\delta^{18}O_P$ natural abundance had to rely on Hedley HCl extraction, otherwise the isotopic signals were impacted by the presence of organic matter and sesquioxides. The first results, however, then showed that soil $\delta^{18}O_P$ values were in the range common for isotope equilibrium in the top first 60 cm of the soil profile. There was also no systematic deviation of the soil $\delta^{18}O_P$ value between bulk and rhizosphere soil. At site MItterfels this trend even continued to 2 m soil depth. However, below 60 cm (Vessertal) to > 150 cm (Conventwald), we also found soil $\delta^{18}O_P$ values that were significantly smaller. The analyses are still in progress, and also extended to 30 m depth in sediment samples on selected sites. Nevertheless, the current data already indicate that there appear to be site-specific options to cope with P deficiency in the surface soil, indicated by a different degree of P transformation and cycling in the subsoil.

Microbial biomass stoichiometry and mineralization of organic carbon, nitrogen and phosphorus

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Soil microorganisms play an important part in the turnover of organic carbon (C), nitrogen (N) and phosphorus (P) in forest ecosystems. Ecological stoichiometry deals with the C:N:P ratios of organisms and their resources to obtain knowledge about the cycling of these elements. Stoichiometric relationships can give insights into processes like litter decomposition or microbial mineralization of organic C, N and P. We studied microbial biomass stoichiometry and microbial community composition in the A and B horizons of two temperate forest Cambisols with contrasting P availability (Unterluess and Bad Brueckenau). In an incubation experiment, C, N and P were added to the soils in a full factorial design. Microbial biomass C, N and P concentrations were analyzed by the fumigation-extraction method and microbial community composition was analyzed by a community fingerprinting method (automated ribosomal intergenic spacer analysis, ARISA). Microbial biomass C:N:P stoichiometry changed more strongly due to element addition in the P-poor soils, than in the P-rich soils. The microbial community composition analysis showed that element additions led to stronger changes in the microbial community in the P-poor than in the P-rich soils. Therefore, the changed microbial biomass stoichiometry in the P-poor soils was likely caused by a shift in the microbial community composition.
It is still under discussion whether the C:N:P ratio or the organic C quality of litter is the main driver for microbial litter decomposition. To assess this question, we are planning an incubation experiment with Oi and Oe layers of beech, spruce, pine and mixed deciduous forests. Organic C, N and P net mineralization rates will be analyzed by quantification of inorganic N and P, dissolved organic C and N as well as respiration measurements by an automated respirometer. The results will be linked to C:N:P stoichiometry and organic C quality of the litter. We hypothesize that net mineralization of N and P is more closely related to litter C:N:P stoichiometry than to organic C quality, while net C mineralization is mainly determined by the organic carbon quality.
Acknowledgement: We are grateful to the DFG for financial support to SP1389/4-1 in the framework of the SPP 1685.

Epigenetic adaptation and memory in *Populus trichocarpa*

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Phosphate limits total biomass production in natural ecosystems. Due to low mobility of phosphate, higher plants require special adaptations for P acquisition. The genetic and physiological basis of this adaptation is well-investigated. Largely unknown, however, is the extent to which epigenetic modifications play a role. These may allow more rapid adaptations to environment-related stresses than mutational changes. In this study, it was analyzed whether clonal *Populus trichocarpa* cuttings, grown on four different locations in Germany, "memorize" their host site and previous P availability. First, the P concentration in soils and plants was determined to record tree background history. Based on these results, cuttings from two different sites with adequate and low P availability were selected. These were grown in hydroponic culture with different P levels. Additionally, genome-wide epigenetic adaptations based on DNA methylation differences were quantified using BS-Sequencing. In particular, it was analyzed whether DNA methylation differences occurred preferentially in P nutrition-related genes and correlate with P acquisition. Therefore, gene expression patterns of differentially methylated gene candidates were obtained by qPCR. Eventually, it was discussed whether dynamic DNA methylation may be responsible for site adaptations and growth performance in perennials.

Phosphorus fractions in preferential flow pathways in forest soils

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In our SPP 1685 project, we investigate phosphorus (P) forms in preferential flow pathways in forest soils. Following the hypothesis of the SPP 1685 that P depletion of soils drives forest ecosystems from P acquiring systems (efficient mobilization of P from the mineral phase) to P recycling systems (highly efficient cycling of P), we take samples at the SPP core sites whose soils differ in their availability of mineral bound P. In our experiments, we use tracer experiments to identify potential subsurface transport paths through the soil profile and analyze the flow patterns using digital image analyzing tools. Soil samples are taken from stained (flow region) as well as unstained (non-flow region) compartments. They are analyzed for P fractions using a modified Hedley fractionation scheme.
The poster presents results of the chemical P fractions in preferential flow pathways compared to soil matrix for different SPP core sites.

Sugar efflux in *Picea abies* ectomycorrhizas

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A mutualistic exchange of phosphate and carbohydrates is common to ectomycorrhizal (ECM) symbiosis. In poplar, certain members of a gene family coding for novel sugar facilitators. SWEETs, are induced upon ectomycorrhiza formation, suggesting a direct link between these proteins and fungal carbon nutrition in symbiosis. We have addressed the question, whether ectomycorrhiza-dependend induction of SWEET gene expression is also found in the gymnosperm *Picea abies*, for which a genome sequence is available.
We were able to identify 51 putative members of the SWEET gene family in the *P. abies* genome. Compared to *Arabidopsis with* 17 (Chen et al. 2010) and poplar with 27 members (Nehls, unpublished) of the SWEET gene family, the number of potential sugar facilitators is much higher in the conifer. However, for 12 of the respective *P. abies* SWEET genes only truncated proteins could be deduced, indicating a large number of pseudogenes in the Norway spruce genome. Based on primary protein sequence, the members of the gene family can be divided into four subgroups. Up to now, only the expression of members of subgroup I was affected upon plant interaction with either pathogenic or symbiotic organisms. With 21 members found in the Norway spruce genome, the SWEET subgroup I of *P. abies* contains many more members than those of *Arabidopsis* (two members), poplar, or *Picea glauca* (6 members, each). In contrast, no Norway spruce homologs of subgroup 3 (8 members in poplar and seven in *Arabidopsis*) were found. Similar high numbers of Norway spruce homologs as present in poplar, *P. glauca* and *Arabidopsis* were found for subgroups II and IV.
We have compared SWEET gene expression in non-mycorrhized fine roots and mycorrhizas for all (39) *P. abies* members of subgroups I, II and IV. We were able to amplify respective DNA fragments for 16 *P. abies* SWEET genes and quantify their transcript levels by qRT-PCR. However, none of the investigated Norway spruce SWEET genes revealed differential gene expression in mycorrhized compared to non-mycorrhized fine roots. This result is discussed in the background that in *Pinus* ectomycorrhiza regulated SWEET gene expression was observed.

Potential bioavailability of nanoparticulate and colloidal bound P

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Phosphorus (P) is an essential but often limiting nutrient in ecosystems. With progressive ecosystem and soil development, phosphorous rocks and primary minerals are depleted as source of phosphate (PO_4^{3-}). Thus, ecosystems change from P acquiring to recycling systems. In recycling systems the bioavailability of phosphate is linked to the mobilization via enzymatic catalyzed hydrolysis. The aim of this study is to determine how organisms counteract P losses from ecosystems by analyzing the potential bioavailability of P associated to nanoparticles and fine colloids of recycling ecosystems. It is hypothesized that the enzymes not only hydrolyze single P containing organic molecules but also the phosphate from P containing organic molecules within or on nanoparticles (NP, 1 – 100 nm) and fine colloids (FC, >100 – 450 nm). NP and FC overlap with the operationally defined dissolved phase and have furthermore proven to bind a majority of the P below 0.45µm.
In order to simulate the P passage of a root membrane, an equilibrium dialysis machine with dialysis cells separated by a 1kDa membrane was used. Three types of enzymes (acid phosphatase for monoester, a 1:1 mix of nuclease and DNase for diester and phytase for IHP) together with corresponding model substances were used. After this, soil extracts and stream water from defined SPP-locations served as environmental samples. Inductively coupled plasma mass spectrometry (ICP-MS) served for the detection of released phosphate, through an organic carbon detector (OCD) the membrane passage of whole molecules were controlled and dynamic light scattering (DLS) was used for NP and FC size measurements.
Enzymes also hydrolyzed phosphate that was bound to the surface of NP and FC and it was possible to give information about the primary binding forms of phosphate within nanoparticles and fine colloids.

Humus form specific relationships between water extractable phosphorus (P), microbial biomass P and P mineralization rates in the forest floor and foliar P contents of European beech

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The decomposition of fallen litter is a central process in the P cycle of forest ecosystems. Depending on faunal activity, these decomposition processes take place in different soil compartments, which is reflected in different humus forms. Forest floors of moder sites are presumably more important for tree P nutrition than those of mull sites. Our hypotheses were (i) that the stocks of water-extractable P [P_{water}] and microbial biomass P [P_{mic}] are higher in forest floors of moder-sites than in those of mull-sites and (ii) that contents and stocks of P_{water} and P_{mic} as well as P mineralization rates in forest floors are more closely correlated to foliar P contents of European beech (*F. sylvatica*) at moder than at mull sites.

The forest floors of 10 mull and 10 moder sites were sampled four times between 2012 and 2014. P_{water} was extracted from field-moist samples; P_{mic} was determined by chloroform-fumigation-extraction using water as extractant and a k_{EP} value of 0.40. P mineralization rates were determined from an 8-week-incubation trial at 20° C. Foliar P contents of beech trees were determined yearly from 2012 to 2014.

On average across all sampling dates, stocks of P_{mic} in forest floors of moder sites significantly exceeded those determined in the forest floors of mull sites (t-test, $p < 0.001$). In contrast, stocks of P_{water} in the forest floor did not differ significantly between moder and mull sites ($p = 0.08$). For the moder sites, we found a close positive correlation between P_{mic} contents in the forest floor and foliar P contents ($R^2 = 0.79$, $p < 0.001$). Additionally, on these sites foliar P contents were significantly positively related to P_{water} contents ($R^2 = 0.67$, $p < 0.01$), P_{water} stocks ($R^2 = 0.61$, $p < 0.05$) and P mineralization rates (expressed on an area basis; $R^2 = 0.72$, $p < 0.01$) but not to P_{mic} stocks. For the mull sites, we only found a significant relationship between foliar P contents and the contents of P_{water} in the forest floor ($R^2 = 0.42$, $p < 0.05$).

Hypothesis (i) is only partly supported. Stocks of P_{water} in the forest floor varied strongly among individual sites which could have masked humus-form-specific differences. Hypothesis (ii) is supported by our data. Positive relationships between foliar P contents and P_{water} stocks as well as P mineralization rates in the forest floor of moder sites support the role of moder forest floors in supplying trees with plant available P. The P_{mic} content of the forest floor was the best predictor for the foliar P content and might therefore be a useful indicator to assess the P-nutritional status of beech on moder sites. Yet, the absence of a significant correlation between foliar P contents and P_{mic} stocks indicates that P_{mic} may not simply be regarded as a more or less "plant available" P fraction.

Seasonal analysis of P uptake and ectomycorrhizal diversity in young beech trees

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Understanding phosphorus dynamics in temperate forests is crucial to developing a better model for ecosystem functioning and forest management strategies. However, until now, only limited knowledge exists on the seasonal variation of the link between ectomycorrhizal (EM) species diversity and P demand or P uptake in young beech trees. To investigate this, 150 young beech trees were excavated from two contrasting research sites containing high (Bad Brückenau, Germany) and low (Unterlüss, Germany) levels of available P in autumn 2013, respectively. Seasonal pulse labeling under controlled conditions using ^{33}P-orthophosphate was performed at five phenological stages over the course of the year. Plants from each site were harvested during each developmental stage at day 1, 7 and 30 after labeling. Subsequently, analyses of ^{33}P in all aerial parts of the plant and the fine roots, coarse roots including ectomycorrhizal root tips were conducted. Moreover, the specific ^{33}P activity in the microbial biomass was assessed. Preliminary analysis of results showed that plants from Unterlüss took up higher amounts of ^{33}P during each developmental stage. Also, the ectomycorrhizal community displayed higher uptake of radioactive label during each phenological stage in Unterlüss. The ^{33}P uptake into the microbial biomass occurred during the first day after the labeling and the specific ^{33}P activity was relatively stable during the following 30 days. The mycorrhizal diversity was influenced by seasonality with only one morphotype (*Cenococcum geophilum*) having been found throughout the year. Further analysis of the data is needed in order to develop a model linking EMF species abundance and P acquisition with plant uptake and phenology.

References:

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Biologically-released phosphate in soil under young beech trees (*Fagus sylvatica* L.) at two sites differing in soil P availability

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Biotic and abiotic processes involved in phosphorus (P) nutrition of trees have not yet been disentangled. Our objective was to assess the release of biologically cycled phosphate – labeled through the addition of $H_2{}^{18}O$. We established a pot experiment with one year old beech trees planted in soil either with or without the organic layer from Lüss and Bad Brückenau on April 24th, 2014. After 77 days of regular irrigation with tap water, we applied $H_2{}^{18}O$ (200 ‰) to the pots. After 0h, 6h, 24h, 2d, 3d, 6d, 10d, 22d we destructively harvested the pots. We measured resin-extractable P and the potential activity of phosphomonoesterase and –diesterase as well as the microbial phosphorus concentrations. Enzyme activities should be related to phosphate release from organically-bound P associated with the exchange of O atoms in phosphate by the ^{18}O label in ambient water in the pots. Oxygen isotope ratios in phosphate ($\delta^{18}O_P$) are currently being measured and are intended to be presented in conjunction with enzyme activities and microbial phosphorus concentrations.

Plant-induced chemical changes in the rhizosphere of *Fagus sylvatica* seedlings depending on soil P speciation and tree provenance

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Trees contribute to P cycling in forest ecosystems by litter deposition and P mobilizing root activities. In our study, we address the question how well trees can adapt their exudation pattern to changing P availability. We hypothesize, that P mobilizing activity of the plant is restricted to specific root segments – affecting respective micro zones in the rhizosphere - and depends on the internal demand for P. It is the latter, in combination with the genetic background (provenance) that determines the exudation pattern of the roots. Accordingly, the transfer of seedlings from a soil with a high level of plant available P to a soil with less available P and vice versa will affect exudation rates of potentially P solubilizing agents (increase/decrease in: acid phosphatase activity, exudation of organic acid anions and protons). However, this transfer will not cause a change in the exudation pattern that would fit the local P speciation and availability.

In a preliminary experiment we planted tree seedlings from a Pi deficient site (obtained from a plant nursery) to a Pi sufficient soil (Bad Brückenau, BB) in rhizoboxes. When the root system was developed, soil micro zones around specific root segments were analyzed. The pH and phosphatase activity pattern were measured by optodes and zymography, respectively. Exuded organic acid anions were collected with filter papers and soil solution with suction cups. Soil P speciation was investigated by Hedley fractionation. In addition, the P status of the plant was assessed by quantifying the P content and acid phosphatase activity in leaves.

For the ongoing main experiment we planted tree seedlings collected from the BB and Lüss sites, each in both types of soil (BB, Lüss). In addition, we started an experiment with seedlings grown from seeds collected at the BB and Vessertal (VT) sites and planted in BB, VT and Lüss soil. Upon development of the root system, measurements will be performed as in the preliminary experiment.

We will present results from the preliminary experiment - focusing on methodological aspects - and first results from the ongoing experiments.

Factors controlling P mobility in the soil under a beech stand

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Its pivotal role in cell composition and energy transport functions makes phosphorous (P) an essential element for all organisms. To maintain P supply for plant nutrition, its mobilization from P pools to the soil solution is necessary. Little is known about factors influencing the mobility and spatial patterns of water-extractable P and phosphate (PO_4), which are assumed to indicate easily accessible P in the soil.

We investigated small-scale heterogeneity of P species and dissolved organic carbon (DOC) influenced by drying of soil samples, soil depth and distance from the tree stem in a forest soil.

Drying decreased the extractability of total P (P_{tot}) and of PO_4 in the organic layer, whilst in the mineral layer it led to an increase in P_{tot} and a decrease in PO_4. Our results indicate that drought may decrease P availability. This issue has to be emphasized in context of harmonization of extraction methods, and of climate change predictions as well as regarding the assessment of the organic layer for forest nutrition. Concentrations of water-extractable P_{tot}, PO_4 and DOC decreased significantly with every depth level, most evident between the organic and the mineral soil. Furthermore the composition of water-extractable P_{tot} changed with depth: in the organic layer the largest share of P_{tot} was PO_4 while in the mineral soil the organic and colloidal P fractions were largest. This highlights the importance of the organic layer for plant nutrition because water-extractable PO_4 can be directly taken up by plants. Small-scale heterogeneity could not be explained by distance from the tree. We did not detect a clear spatial pattern in the horizontal distribution of P and DOC concentrations.

Are phosphorus patterns in forest soils influenced by the distance from European beech and Norway spruce stems?

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The influence of different tree species on forest soils has been subject to a number of studies that broadly agree on the importance of stemflow for the formation of patterns in the soil chemical composition under European beech (*Fagus sylvatica*), whereas stemflow does not significantly influence soils under Norway spruce (*Picea abies*). As a result, different soil chemical and soil biological patterns and their relation to the stem distance were described, most notable a decrease in pH close to the stem. This pH pattern can be expected to decrease the plant available phosphorus content close to the stem basis of beech.

The objective of the present study was to identify such stemflow induced patterns under beech in comparison with spruce and assess their meaning for forest ecosystems. Volumetric soil samples were taken in 10 cm, 50 cm, 100 cm and 200 cm distance from beech and spruce stems with a root auger in the protected forest "Conventwald" in southwest Germany. The pH (H_2O), pH ($CaCl_2$) and C/N ratio, as well as the total H^+ ion stock, total citric acid extractable phosphorus (P_{tc}), phosphate (PO_4), organic phosphorus (P_o), Al, Fe and Ca contents of the samples were determined and analysed in linear mixed effects models with stepwise backward elimination of non-significant predictor effects (tree species, horizon type and stem distance).

A significant stem distance related P_{tc} pattern could be observed. Other significant gradients were found for the pH (H_2O), pH ($CaCl_2$), total H^+ content, and the C/N ratio. However, none of these patterns could be assigned to stemflow with certainty, because they were encountered under both tree species. Furthermore, the results of this study emphasize that P availability is a complex function of many different soil chemical properties, including the Al and Fe contents, and that pH alone cannot be regarded as a sufficient parameter for the prediction or evaluation of P bioavailability, because a contradicting negative correlation between pH and P_{tc} was found.

The interplay of biodiversity and phosphorus in temperate forests – insights from a database analysis, a field study, and a greenhouse experiment

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In the face of declining phosphorous soil stocks and almost exploited natural raw phosphate deposits, the understanding of the phosphorus (P) nutrition and use efficiency of relevant forest trees is pivotal to maintain future timber production. In tropical forest, it is well-known that increased biodiversity is often closely linked to naturally P depleted soils as plant diversity is expected to enhance the ecosystem's P nutrition owing to niche complementarity. However, little is known about the interplay between phosphorus in soil and biomass, P use efficiency (PUE) of relevant forest trees and biodiversity in temperate forest ecosystems. To shed light on the mechanisms of temperate forest P nutrition, we conducted analyses of a huge array of data from databases, field studies, and greenhouse experiments.

Here we show the results of selected beech and spruce forest ecosystems from the German-wide database BZEII (Second National Forest Soils Inventory). The analysis aimed to reveal (1) the fundamental relationship between biodiversity and P-related variables in leaf biomass, humus and soil using correlation analysis and to (2) model different PUE indices (PUPE: P uptake efficiency; PUTE: P utilization efficiency; PRE: P recycling efficiency) in response to further environmental variables (site, forest stand, and soil parameters) using boosted regression tree analysis (BRT). In particular, we hypothesized that—similarly to tropical ecosystems—biodiversity decreases with increasing P content in soil **(H1)** and that the P nutrition status and the P use efficiency measures of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst) increases with biodiversity **(H2)**.

Statistical analysis revealed complex correlations, with the interplay of biodiversity and considered P-related variables in spruce forests being closer related than in beech forests. Moreover, biodiversity indices belonged to the most important drivers explaining the P nutrition status of beech (Simpson-Index of the shrub layer), the PRE of spruce (Richness moss layer), the PUTE of spruce (Evenness shrub layer), and the PUTE of beech (Shannon-Index of field and shrub layer combined).

In spruce forests, the diversity of the tree layer was negatively related to P soil content (support for H1). Yet the diversity of the field and moss layer was positively related with the P content in soil and humus (rejection of H1).

Considering the P nutrition status of beech and the shrub layers' biodiversity our hypothesis H2 holds true—in contrast to the PRE of spruce, which was negatively related with the moss layers' diversity. Accordingly, the PUTE of spruce and beech were negatively related to the diversity in the shrub layer.

Our study supports two main insights: (1) Significant relationships between P and biodiversity exist in temperate forests; (2) Yet universal relationships between P and biodiversity of temperate forests are missing since these relationships vary among forest ecosystems, vegetation layers, and the P component (content or stock, humus or soil).

Spatial distribution of Arbuscular mycorrhiza in a non-typical environment

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Community composition or structure is driven by a range of different biotic and abiotic factors that can exert influences at broadly different spatial and temporal scales (Rillig and Mummey, 2006). Beech forests are traditionally considered ectomycorrhizal systems, but AMF-hosts plants often grow patchy in the understory, being dependent on AM fungi for P uptake (Postma et al., 2007). Understanding of the spatial patterns of AMF mycelia is needed to interpret species diversity and nutrient fluxes. Spatial distribution of AMF fungi in an ectomycorrhiza dominated ecosystem, where potential hosts are isolated, will be related to the distribution of the understorey plants.

So we assume, that AMF distribution also is similar and they are distributed as islands in the "desert" of non-host plants.

Spatial distribution of AMF spores could be shown as a function of spatial distances to the next potential plant host in the sampled beech forest with a sharp decrease within the first 20 cm to the host. This reflects the dependency of AMF on potential hosts, which are isolated in these forests: strong concentration of AMF close to host plants!

Notes

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