Rostock. Meeresbiolog. Beitr.	Heft 26	25-33	Rostock 2015

Anastasia Bragina[1], Christina Müller[2] & Gabriele Berg[1,2]

[1]Institute of Environmental Biotechnology, Graz University of Technology, 8010 Graz, Petersgasse 12, Austria, gabriele.berg@tugraz.at
[2]Austrian Centre of Industrial Biotechnology (ACIB GmbH), Petersgasse 14, 8010 Graz, Austria

The moss microbiome: new insights into the microbial world of plants and its biotechnological potential

Abstract

Mosses have a key position in the evolution of green plants and are used as model organisms to understand plant development and genetics as well as the plant microbiome. Here we summarize the knowledge about the moss microbiome with special focus on the genus *Sphagnum*. *Sphagnum* mosses harbor a highly diverse microbiome with essential functions for the host including nutrient supply, growth promotion and stress protection. Moreover, moss-associated bacteria fulfill important functions for the whole (bog) ecosystem: they are able to oxidize methane and form a cooling net on the bog surface. All the unique properties of the moss microbiome are an immense treasure box for biotechnology.

Zusammenfassung

Moose haben als erste Landpflanzen eine Schlüsselstellung in der Evolution der Pflanzen und werden deshalb als Modellorganismen für Untersuchungen zur Pflanzenentwicklung und –genetik sowie des Mikrobioms herangezogen. In diesem Artikel diskutieren wir die Struktur und Funktion des Moosmikrobioms mit einem speziellen Fokus auf die Gattung *Sphagnum*. Diese moorbildenden Moosarten enthalten ein vielseitiges Mikrobiom, was für essentielle Funktionen wie Nährstoffversorgung, Wachstumsförderung und Stressschutz verantwortlich ist. Darüber hinaus kommt dem *Sphagnum*-Mikrobiom eine wichtige Bedeutung für das gesamte Ökosystem zu; Bakterien oxidieren Methan und bilden somit ein wichtige Schutzschicht für unser Klima. All diese einzigartigen Eigenschaften machen das Moosmikrobiom zu einer Schatzkiste für die Biotechnologie.

Keywords: moss microbiome, Sphagnum, biotechnology

This manuscript is dedicated to Prof. Dr. Helmut Pankow, who was the teacher and diploma supervisor of G.B. and a great friend of the small plantlets like algae and mosses.

1 The plant microbiome and mosses as model organisms

Plants have recently been recognized as meta-organisms due to a close symbiotic relationship with their microbiome (BULGARELLI et al. 2012; LUNDBERG et al. 2012; HIRSCH & MAUCHLINE 2012). Comparable to humans and other eukaryotic hosts, plants also harbor a “second genome” that fulfils important host functions (BERG 2009; BERG et al. 2013). These findings were driven by both ‘omic’-technologies guided by next-generation sequencing (NGS) and microscopic advances (JANSSON et al. 2012; CARDINALE 2014). The rhizosphere was already defined by LORENZ HILTNER in 1904 as root-surrounding soil influenced by root exudates (HARTMANN et al. 2008). This microenvironment is of central importance not only for plant nutrition, health, and quality, but also for microorganism-driven carbon sequestration, ecosystem functioning, and nutrient cycling in terrestrial ecosystems (MENDES et al. 2012; BERG et al. 2014). The colonization of the root by microbes is triggered by a complex interplay between soil, root exudates, plant defense signaling, and inter-microbial competition (BAIS et al. 2006; DOORNBOS et al. 2012). Root-associated microorganisms, especially mycorrhizal fungi, have played a decisive role in establishment and evolution of terrestrial plants due to enhanced nutrient recovery, plant stress tolerance, and pathogenic resistance. The phyllosphere is also an important habitat because it connects the above-ground part of the plant with its environment (VORHOLT 2012). Although the phyllosphere of several plant species has already been extensively studied, less is known about their microbial diversity, which could be influenced by different surface structures, antimicrobial waxes and other plant defense mechanisms. The highly specific plant-associated niche is occupied by endophytes that establish diverse metabolic interactions with their host and support plant growth and health (BERG et al. 2005). Moreover, plants were suggested to select competent endophytes from the environment for their own ecological benefit.

Plants are complex organisms with the largest genomes known, and, they are divided into different phylogenetical branches. Mosses − the phylogenetically oldest land plants − were identified as important models to study plant development and genetics as well as the moss microbiome due to their unique features. Mosses have evolved alternating generations from a purely haplontic life cycle and, therefore, have a key position in the evolution of green plants. Moss plantlets spend their life cycle mainly as gametophytes in a haploid state, while the sporophyte represents the diploid phase. Mosses can be easily cultured in fluid media and bioreactors allowing the application of experimental techniques similar to those used for microbes and yeast (DECKER & RESKI 2007). Their development is relatively simple, and they generate only a few tissues that contain a limited number of cell types. Although most of the mosses lack vascular tissue, true roots/stems/leaves, flowers and seeds, many signaling pathways found in angiosperms are intact in moss (rev. in COVE et al. 2009). The moss *Physcomitrella patens* is an important model organism; it has been used as an experimental organism for more than 80 years and, within the last 15 years, its use as a model to explore plant functions has increased enormously (rev. in COVE et al. 2009). Besides *Physcomitrella*, *Ceratodon purpureus*, *Funaria hygrometrica* and *Sphagnum* spp. have been used as model organisms (WHINAM & COPSON 2006; JASSEY et al. 2011).

2 *Sphagnum* mosses and ecosystems and their specific microbiome

Mosses of the genus *Sphagnum* are among the most abundant and cosmopolitan vegetation of bogs in the Northern hemisphere and greatly contribute to both global carbon turnover and global climate. The ecological significance of bogs is directly related to the physical, morphological and chemical characteristics of *Sphagnum* peat mosses, which sets *Sphagnum* apart from other mosses at practically every stage of the life cycle (DANIELS & EDDY 1985). Moreover, *Sphagnum* mosses are able to change their environments: living Sphagna have extraordinarily high cation exchange capacity and therefore acidify their environment by exchanging tissue-bound protons for basic cations in surrounding water (SOUDZILOVSKAIA et al. 2010). Bog ecosystems belong to the oldest vegetation forms, with more or less constant conditions for thousands of years (SUCCOW & JOOSTEN 2001). They cover 4 million km^2, approximately 3% of the earth's surface, and have a high value for biodiversity conservation, as reservoir of fresh water, for human welfare, and our world climate due to their extraordinary role in carbon sequestration (RAGHOEBARSING et al. 2005). The latter resulted in a net cooling effect on the global radiation balance (DISE 2009). Besides, these long-existing ecosystems are extremely sensitive to changing abiotic factors connected with climate change (STRACK 2008; DISE 2009). When peatlands degrade, their stored carbon is released. For example, drainage of peat soils results in CO_2 and N_2O emissions of globally 2–3 Gt CO_2-eq per year (JOOSTEN & COUWENBERG 2009).

In the past, research interest was mainly attracted by the microbial populations involved in CH_4 cycling and colonizing mostly dead Sphagna (DEDYSH et al. 1998, 2001; HORN et al. 2003, TUOMIVIRTA et al. 2009), and in the cultivation of uncultured bacteria (DEDYSH 2011). Now, there are several reports on specific bacterial groups associated with the living Sphagna, e.g. methanotrophic symbionts (RAGHOEBARSING et al. 2005; LAMORLA et al. 2010; KIP et al. 2011; PUTKINEN et al. 2012, LARMOLA et al. 2014) since *Sphagnum* mosses were identified as indicators for climate change (WHINAM & COPSON 2006; JASSEY et al. 2011). Recently, we showed that living *Sphagnum* mosses are colonized in high abundance with specific microorganisms (OPELT et al. 2007a; BRAGINA et al. 2012a). Due to the fact that this phylogenetically old plant group has no roots, the leaf-associated bacteria fulfil important functions like nutrient supply and pathogen defense for moss growth and health (OPELT et al. 2007b, c). During the last years we investigated microbial communities of several cosmopolitan *Sphagnum* species in Austrian and Russian bogs with a special focus on their ecology and potential for biotechnological applications. Host specificity of moss-associated microbiomes was detected independent of geographic region at both structural and functional levels (BRAGINA et al. 2012b, 2013). The degree of host specificity varied between distant and closely related moss species and corresponded to spectra of secondary metabolites produced by plants (OPELT et al. 2007c; BRAGINA et al. 2012b). Moreover, environmental factors such as acidity and nutrient richness were defined as the main ecological drivers for microbial diversity. We showed that plant specificity of functional bacterial groups is determined by their role within the ecosystem (BRAGINA et al. 2013). Furthermore, visualization of the intact plant-microbial consortia revealed dense and well-structured microbial colonization patterns in/on *Sphagnum* plants, and showed that stems and leaves of mosses were occupied by various taxonomic groups of bacteria (Fig. 1). *Sphagnum* leaves consist of a network of (dead) hyalocysts and (living) chlorocysts. Although the hyalocysts are densely colonized by bacterial cells, they are closely connected to the photosynthetically active chlorocysts (Fig. 1). Notably, we showed that associated microbial communities are maintained during the entire lifecycle of the host plants which contributes to the host specificity (BRAGINA et al. 2013). Additionally, the core microbiome not only contained mostly potential beneficials, but was also shared between the moss generations and transferred within the spore capsules. These facts emphasize the importance of the microbiome for mosses as the phylogenetically oldest land plants on Earth.

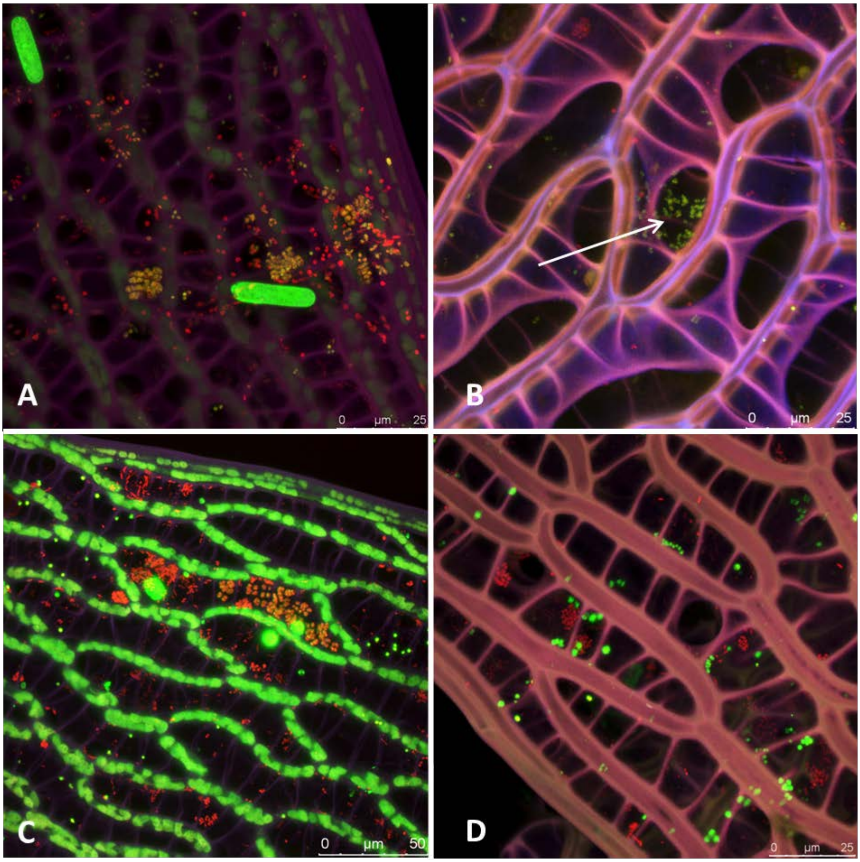

Fig. 1 The moss microbiome visualized by Fluorescence *in situ* hybridization and confocal laser scanning microscopy. A) Phyllosphere of a *Sphagnum* leave showing the network of cells combining hyalocysts and chlorocysts as well as *Alphaproteobacteria* (yellow), bacterial colonies (red) and eukaryotic organisms, B) Phyllosphere of a *Sphagnum magellanicum* leave showing *Alphaproteobacteria* (yellow) and other bacterial colonies (red) C) phyllosphere of a *Sphagnum fallax* leave showing *Planctomycetes* (yellow) and other bacterial colonies (red), D) Phyllosphere of a *Sphagnum magellanicum* leave showing *Planctomycetes* (yellow) and other bacterial colonies (red).

3 Exploiting the first moss metagenome

A high functional diversity within the *Sphagnum* microbiome applying an Illumina-based metagenomic approach followed by *de novo* assembly and MG-RAST annotation was identified (BRAGINA et al. 2014). An inter-environmental comparison revealed that the *Sphagnum* microbiome harbors specific genetic features that distinguish it significantly from microbiomes of higher plants and peat soils. The differential traits especially support an ecosystem functioning by a symbiotic life style under poikilohydric and ombrotrophic conditions. In accordance to a plasticity-stability balance, we found abundant metagenomic subsystems responsible to cope with oxidative and drought stresses, to exchange (mobile) genetic elements, and genes that encode for resistance to detrimental environmental factors, repair, and self-controlling mechanisms. Multiple microbe-microbe and plant-microbe interactions were also found to play a crucial role as indicated by diverse genes necessary for biofilm formation, interaction via quorum sensing and nutrient exchange. A high proportion of genes involved in nitrogen cycle and recycling of organic material supported the role of bacteria for nutrient supply. 16S rDNA analysis indicated a higher structural diversity than previously detected by PCR-dependent techniques. The *Sphagnum* microbiome possesses a highly versatile genetic potential for sustainable functioning in association with the host plant and within the peatland ecosystem.

4 The biotechnological potential of moss-associated bacteria

Bioprospecting is the process of discovery and commercialization of new products based on biological resources (STROBEL & DAISY 2003). Plants and their associated microorganism constitute a rich source of such valuable bioactive natural products. In the recent time we have demonstrated that the moss microbiome is a promising bio-resource for environmental biotechnology – with respect to novel bioactive substances, biocatalysts or stress-protecting bacteria. It represents a habitat underlying extreme environmental conditions, a feature that allows the discovery of extraordinary metabolic capabilities or unknown enzymes. Currently we are investigating the potential biotechnological application of moss-associated bacteria for sustainable agriculture and green biotechnological processes.

The use of isolated microorganisms or microbial consortia as biological control agents (BCAs) is a promising alternative to conventional agricultural techniques (BERG et al. 2013), and in the case of the moss microbiome, this was shown especially for stress protection and growth promotion of economically relevant crops (ZACHOW et al. 2013). Several endophytic bacterial isolates, belonging mainly to the genera *Burkholderia*, *Pseudomonas*, *Flavobacterium*, *Serratia* and *Collimonas,* were able to colonize and promote plant growth (SHCHERBAKOV et al. 2013). Other isolated bacterial strains (mainly *Pseudomonas* sp.) demonstrated high potential as stress protection mediators, displaying good growth under several stress conditions (low temperature, desiccation and oxidative stress resistance) (ZACHOW et al. 2013).

The moss microbiome demonstrates likewise great potential for the discovery of novel biocatalytic enzymes that can be employed in sustainable industrial processes, for example for production of pharmaceuticals. Enzymatic reactions are in general environmentally benign when compared to traditional chemical synthesis routes (FERRER et al., 2005). Besides, high selectivity and a diverse product scope make the discovery of new enzymes a very attractive research field. The ability of *Sphagnum* species to produce numerous bioactive secondary metabolites, a property that is directly related to its specific microbial colonization, was reported before (BASILE et al. 1999; ZHU et al. 2006). Culture-dependent analysis of *Sphagnum* moss associated endo- and ectophytic bacteria indicated a high occurrence of antifungal and to a lesser extent of antibacterial isolates (OPELT et al., 2007c). However, the majority of the microbial population in the investigated mosses (up to 97 %) is not accessible by current cultivation methods. Metagenome mining circumvents this problem, offering the possibility to discover new enzymes from uncultured microbes (FERRER et al., 2005). As part of our *Sphagnum* moss metagenomic approach we established a screening platform consisting of a fosmid clone library in *E. coli* to analyze metagenomic sequences of the moss microbiome. Several antibiotic, antifungal and anticancer agents of microbial origin are synthetized by large multi-modular enzymes, such as non-ribosomal peptide synthetases (NRPSs) and polyketide synthases (PKSs) (WALSH 2008). Screening for PKS and NRPS genes by PCR-amplification in the clone library, combined with *in silico* analysis of the metagenomic database, revealed high diversity of the targeted enzymes. Especially, the identified NRPS gene sequences revealed identities ranging from 47 to 99.4% to the closest homologs in GenBank, belonging mainly to the bacterial phyla *Proteobacteria* and *Actinobacteria* (MÜLLER et al., pers. communication). The occurrence of other industrially relevant enzyme classes in the *Sphagnum* microbiome – such as decarboxylases, lipases and phosphatases - was also demonstrated by further screening approaches. A novel moss metagenomic decarboxylase, showing a homology of 74% with a polyprenyl-4-hydroxybenzoate decarboxylase from *Ralstonia* sp. PBA, could be isolated and is currently being evaluated as a novel biocatalyst for enzymatic carboxylation processes (MÜLLER et al., pers. communication). To date, most of the studied microbiomes for enzyme mining were originated from soil, the ocean or the human gut (SIMON & DANIEL 2011). However, exploitation of the plant-associated microorganism has been underrepresented so far. The moss microbiome demonstrates not only high versatility of its inhabitants but also an enormous potential - a treasure box - for biomedical, biotechnological and agricultural applications.

Acknowledgement

This manuscript was supported by different grants from the Austrian Science Foundation FWF (I183-B16; I 882-B16) to G.B. The cooperation of C.M. and G.B. was funded by a project in the Austrian Centre of Industrial Biotechnology, which has been supported by the Austrian BMWFJ, BMVIT, SFG, Standortagentur Tirol and ZIT through the Austrian FFG-COMET-Funding Program. We also gratefully acknowledge support from NAWI Graz.

References

BAIS, H.P., WEIR, T.L., PERRY, L.G., GILROY, S. & VIVANCO, J.M. (2006): The role of root exudates in rhizosphere interactions with plants and other organisms. - Annu Rev Plant Biol 57: 233–266.

BASILE, A., GIORDANO, S., LÓPEZ-SÁEZ, J.A. & COBIANCHI, R.C. (1999): Antibacterial activity of pure flav,onids isolated from mosses. - Phytochemistry 52: 1479-1482.

BERG, G., KRECHEL, A., DITZ, M., SIKORA, R.A., ULRICH, A. & HALLMANN, J. (2005): Endophytic and ectophytic potato-associated bacterial communities differ in structure and antagonistic function against plant pathogenic fungi. - FEMS Microbiol Ecol 51: 215–29.

BERG, G. (2009): Plant-microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture. - J Appl Microbiol Biotechnol 84, 11–18.

BERG, G., ZACHOW, Z., MÜLLER, H., PHILIPPS, J. & TILCHER, R. (2013): Next-generation bio-products sowing the seeds of success for sustainable agriculture. - Agronomy 3: 648-656.

BERG,G., GRUBE, M., SCHLOTER, M. & SMALLA, K. (2014): Unraveling the plant microbiome: looking back and future perspectives. - Front Microbiol 5: 148.

BRAGINA, A., BERG, C., CARDINALE, M., SHCHERBAKOV, A., CHEBOTAR, V. & BERG, G. (2012a): *Sphagnum* mosses harbour highly specific bacterial diversity during their whole lifecycle. - ISME J 6: 802–813.

BRAGINA, A., MAIER, S., BERG, C., MÜLLER, H., CHOBOT, V., HADACEK, F. & BERG, G. (2012b): Similar diversity of *Alphaproteobacteria* and nitrogenase gene amplicons on two related *Sphagnum* mosses. - Front Microbiol 2: 275.

BRAGINA, A., BERG, C., MÜLLER, H., MOSER, D. & BERG, G. (2013): Insights into functional bacterial diversity and its effects on Alpine bog ecosystem. - Sci Rep 3: 1955.

BRAGINA, A., OBERAUNER-WAPPIS, L., ZACHOW, C., HALWACHS, B., THALLINGER, G.G., MÜLLER, H. & BERG, G. (2014): The *Sphagnum* microbiome supports greatly ecosystem functioning under extreme conditions. - Mol Ecol, 23: 4498-44510.

BULGARELLI, D., ROTT, M., SCHLAEPPI, K., VER LOREN VAN THEMAAT, E., AHMADINEJAD, N., & ASSENZA, F. (2012): Revealing structure and assembly cues for *Arabidopsis* root-inhabiting bacterial microbiota. - Nature 488: 91–95.

CARDINALE, M. (2014): Scanning a microhabitat: plant-microbe interactions revealed by confocal laser microscopy. - Front Microbiol 5: 94.

COVE, D.J., PERROUD, P., CHARRON, A.J., MCDANIEL, S.F., KHANDELWAL, A. & QUATRANO, R.S. (2009): The moss *Physcomitrella patens*: a novel model system for plant development and genomic studies. In: Emerging model organisms: a laboratory manual, Vol. 1. Cold Spring Harbor Laboratory Press: New York.

DANIELS, R.E. & EDDY, A. (1985): Handbook of Europaen Sphagna. Institute of Terrestrial Ecology, Natural Environment Research Council. - Cambrian News: Aberystwyth.

DECKER, E.L. & RESKI, R. (2007): Moss bioreactors producing improved biopharmaceuticals. - Curr Opin Biotechnol 18: 393–398.

DEDYSH, S.N., PANIKOV, N.S. & TIEDJE, J.M. (1998): Acidophilic methanotrophic communities from *Sphagnum* peat bogs. - Appl Environ Microbiol 64: 922–929.

DEDYSH, S.N., DERAKSHANI, M. & LIESACK, W. (2001): Detection and enumeration of methanotrophs in acidic *Sphagnum* peat by 16S rRNA fluorescence in situ hybridization, including the use of newly developed oligonucleotide probes for *Methylocella palustris*. - Appl. Environ Microbiol 67: 4850–4857.

DEDYSH, S.N. (2011): Cultivating uncultured bacteria from northern wetlands: knowledge gained and remaining gaps. - Front Microbiol 2: 184.

DISE, N.B. (2009): Environmental science. Peatland response to global change. - Science 326: 810–811.

DOORNBOS, R.F., VAN LOON, L.C. & BAKKER, P.A. (2012): Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere. - Agron Sustain 32: 227–243.

FERRER, M., MARTÍNEZ-ABARCA, F. & GOLYSHIN, P.N. (2005): Mining genomes and 'metagenomes' for novel catalysts. - Current Opin.Biotechnol 16: 588–593.

HARTMANN, A., ROTHBALLER, M. & SCHMID, M. (2008): Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. - Plant Soil 312: 7–14.

HIRSCH, P.R. & MAUCHLINE, T.H. (2012): Who's who in the plant root microbiome? - Nat Biotechnol 30: 961–962.

HORN, M.A., MATTHIES, C., KÜSEL, K., SCHRAMM, A. & DRAKE, H.L. (2003): Hydrogenotrophic methanogenesis by moderately acid-tolerant methanogens of a methane-emitting acidic peat. - Appl Environ Microbiol 69: 74–83.

JANSSON, J.K., NEUFELD, J.D., MORAN, M.A. & GILBERT, J.A. (2012): Omics for understanding microbial functional dynamics. - Environ Microbiol 14: 1–3.

JASSEY, V.E., GILBERT, D., BINET, P., TOUSSAINT, M.L. & CHIAPUSIO, G. (2011): Effect on temperature gradient on *Sphagnum fallax* and its associated living microbial communities: a study under controlled conditions. - Protist 57: 226–235.

JOOSTEN, H. & COUWENBERG, J. (2009): Are emissions reductions from peatlands MRV- able? Report in: Wetlands International, Ede.

KIP, N., DUTILH, B.E., PAN, Y., BODROSSY, L., NEVELING, K. & KWINT, M.P. (2011): Ultra-deep pyrosequencing if *pmoA* amplicons confirms the prevalence of *Methylomonas* and *Methylocystis* in *Sphagnum* mosses from Dutch peat bog. - Environ Microbiol Rep 3: 667–673.

LARMOLA, T., TUITTILA, E.S., TIIROLA, M., NYKÄNEN, H., MARTIKAINEN, P.J. & YRJÄLÄ, K.. (2010). The role of *Sphagnum* mosses in the methane cycling of a boreal mire. - Ecology 91: 2356–2365.

LARMOLA, T., LEPPÄNEN, S.M., TUITTILA, E.S., AARVA, M. & MERILÄ, P. (2014). Methanotrophy induces nitrogen fixation during peatland development. - Proc Natl Acad Sci USA 111: 734–739.

LUNDBERG, D.S., LEBEIS, S.L., PAREDES, S.H., YOURSTONE, S., GEHRING, J. & MALFATTI, S. (2012): Defining the core *Arabidopsis thaliana* root microbiome. - Nature 7409: 86–90.

MENDES, R., KRUIJT, M., DE BRUIJN, I., DEKKERS, E., VAN DER VOORT, M. & SCHNEIDER, J.H.M. (2012): Deciphering the rhizosphere microbiome for disease-suppressive bacteria. - Science 332: 1097–1100.

OPELT, K., CHOBOT, V., HADACEK, F., SCHÖNMANN, S., EBERL, L. & BERG, G. (2007a). Investigations of the structure and function of bacterial communities associated with *Sphagnum* mosses. - Environ Microbiol 91: 2795–2809.

OPELT, K., BERG, C. & BERG, G. (2007b) The bryophyte genus *Sphagnum* is a reservoir for powerful and extraordinary antagonists and potentially facultative human pathogens. - FEMS Microbiol Ecol 61: 38–53.

OPELT, K., BERG, C., SCHÖNMANN, S., EBERL, L. & BERG, G. (2007c): High specificity but contrasting biodiversity of *Sphagnum*-associated bacterial and plant communities in bog ecosystems independent of the geographical region.- ISME J 1: 502–516.

PUTKINEN, A., LARMOLA, T., TUOMIVIRTA, T., SILJANEN, H.M., BODROSSY, L., TUITTILA, E.S. & FRITZE, H. (2012): Water dispersal of methanotrophic bacteria maintains functional methane oxidation in Sphagnum mosses. - Front Microbiol 3: 15.

RAGHOEBARSING, A.A., SMOLDERS, A.J.P., SCHMID, M.C., RIJPSTRA, W.I.C., WOLTERS-ARTS & DERKSEN, J.M. (2005): Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. - Nature 436: 1153–1156.

SHCHERBAKOV, A.V., BRAGINA, A.V., KUZMINA, E. Y., BERG, C., MUNTYAN, A.N. & MAKAROVA, N.M. (2013): Endophytic bacteria of *Sphagnum* mosses as promising objects for agricultural microbiology. - Microbiology 82: 306–315.

SIMON, C. & DANIEL, R. (2011): Metagenomic analyses: past and future trends. - Appl Environ Microbiol. 77: 1153-1161.

SOUDZILOVSKAIA, N.A., CORNELISSEN, J.H.C., DURING, H.J., VAN LOGTESTIJN, R.S.P., LANG, S.I. & AERTS R. (2010): Similar cation exchange capacities among bryophyte species refute a presumed mechanism of peatland acidification. - Ecology 91: 2716–2726.

STRACK, M. (2008): Peatlands and climate change. International Peat Society: Jyväskylä.

STROBEL, G. & DAISY, B. (2003): Bioprospecting for microbial endophytes and their natural products. - Microbiol Mol Biol Rev 67(4): 491-502.

SUCCOW, M.& JOOSTEN, H. (2001): Lanschaftsokologische Moorkunde. E. Schweizerbart'sche Verlagsbuchhandlung: Stuttgart.

TUOMIVIRTA, T.T., YRJÄLÄ, K. & FRITZE, H. (2009): Quantitative PCR of *pmoA* using a novel reverse primer correlates with potential methane oxidation in Finnish fen. - Res Microbiol 160: 751–756.

VORHOLT, J. A. (2012): Microbial life in the phyllosphere.- Nat Rev Microbiol 10: 828–840.

WALSH, C.T. (2008): The chemical versatility of natural-product assembly lines. - Acc Chem Res 41(1): 4-10.

WHINAM, J. & COPSON, G. (2006): *Sphagnum* moss: an indicator of climate change in the sub-Antarctic. - Polar Record 42: 43–49.

ZACHOW, C., MÜLLER, H., TILCHER, R., DONAT, C. & BERG, G. (2013): Catch The Best – Novel screening strategy to select Stress Protecting Agents for crop plants. - Agronomy 3: 794-815.

ZHU, R.L., WANG, D., XU, L., SHI, R.P., WANG, J. & ZHENG, M. (2006): Antibacterial activity in extracts of some bryophytes from China and Mongolia. - The Journal of the Hattori Botanical Laboratory 100: 603-615.