



Review

Bioprospecting plant-associated microbiomes

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ABSTRACT

There is growing demand for new bioactive compounds and biologicals for the pharmaceutical, agro- and food industries. Plant-associated microbes present an attractive and promising source to this end, but are nearly unexploited. Therefore, bioprospecting of plant microbiomes is gaining more and more attention. Due to their highly specialized and co-evolved genetic pool, plant microbiomes host a rich secondary metabolism. This article highlights the potential detection and use of secondary metabolites and enzymes derived from plant-associated microorganisms in biotechnology. As an example we summarize the findings from the moss microbiome with special focus on the genus *Sphagnum* and its biotechnological potential for the discovery of novel microorganisms and bioactive molecules. The selected examples illustrate unique and yet untapped properties of plant-associated microbiomes, which are an immense treasure box for future research.

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1. Introduction

Bioprospecting is the process of discovery and commercialization of new products based on biological resources (Strobel and Daisy, 2003). A growing need for new bioactive compounds in the pharmaceutical (e.g. antibiotics against multi-resistant pathogens) and the agro- and food industries (e.g. agrochemicals, biocontrol products, food additives) stresses the importance of

prospecting for novel bio-resources (Berg et al., 2013; Woolhouse and Farrar, 2014). Since the chemical diversity of compounds as comprised in biological resources is higher than synthetic chemistry achieves, bio-resources have great potential to hold a manifold of promising compounds for biotechnological application (Bérdy, 2012; Nováková and Farkašovský, 2013). Plants have been described as one of the richest sources of valuable bioactive natural products (McChesney et al., 2007). Progress in the -omics era, including next-generation sequencing (metagenomics, metatranscriptomics) and microscopic advances, has changed our view on eukaryotic hosts and the role of microbial diversity and microbial functions (Jansson et al., 2012; Cardinale, 2014; Mendes and Raaijmakers, 2015). Nowadays, we consider plants,

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like humans and other eukaryotic hosts, as meta-organisms that undergoes a tight symbiotic relationship with their microbiome (Bulgarelli et al., 2012; Hirsch and Mauchline, 2012; Lundberg et al., 2012).

Each plant is colonized by more than 1000 microbial species, which are to a high degree not cultivable. In addition, plants are divided into specific niches for microorganisms, where biotic and abiotic factors shape specific microbial communities. While the rhizosphere has been well-studied for more than 100 years (Philippot et al., 2013), the phyllosphere and especially the endosphere are currently under intense investigation (Vorholt, 2012; Hardoim et al., 2015). Moreover, each plant microbiome has due to the plant-specific secondary metabolism and physiology a specific composition (Berg and Smalla, 2009). This depends on the plant family, for instance dicotyledonous plants have developed a richer secondary metabolism than monocotyledonous plants. Recently it was shown that breeding has a strong impact on the plant microbiome as well, and cultivar-specific effects were identified (Schlaeppi et al., 2014; Cardinale et al., 2015; Pérez-Jaramillo et al., 2015). Thereby, the microbiome fulfils multiple functions for the host health, like pathogen defense and contribution to stress tolerance under adverse environmental conditions and further supports growth and nutrient supply (Berg, 2009; Berg et al., 2013; Bragina et al., 2014; Grube et al., 2015).

While the potential of the microbiome to influence the host is now well-recognized (Blaser, 2014; Berg et al., 2015), the diversity of metabolites that are synthesized by the microbiota is largely unexplored (Berg et al., 2014; Nunes-Alves, 2014). During the last decades it was shown that single cultivable microorganisms represent a plenteous source for novel enzymes and bioactive compounds: around 70,000 natural products derived from microorganisms were reported with almost half of them showing bioactive traits (Bérdy, 2012). Altogether, these facts underline the high diversity of indigenous microbial populations in plant microbiomes, and supports their exploitation for biotechnological purposes, for biocatalytic processes and plant protection, or in the pharmaceutical industry (Harvey, 2008; Duke et al., 2010).

Metagenomics is one means that facilitates examination of the entire genetic pool comprised by (plant) microbiomes, thereby providing access to the potential of the high share of uncultivable microbes. The field of metagenomics has been intensively reviewed in recent time, which illustrates the great interest within the scientific community spanning a wide range of research areas from ecology over medicine to biotechnology (Wang et al., 2014; Banerjee et al., 2015; Coughlan et al., 2015; Cowan et al., 2015; Faust et al., 2015; Garza and Dutilh, 2015; Ravin et al., 2015; Roossinck et al., 2015). Briefly, metagenomics is the study of the combined genomes of all the organisms present at site without culturing them first (Handelsman, 2004). Upon extraction of the total environmental DNA it can either be examined at the sequence level or function driven. Sequence based analysis obviously requires the DNA to be sequenced, which commonly involves random shot gun sequencing (Abbasian et al., 2015). In contrast, when expressed heterologous, the metagenome can be screened for certain, desired activities by subjecting the metagenomic library to specifically designed screening assays (Gabor et al., 2007). Bioprospecting towards novel enzymes and bioactive compounds has been frequently performed using environmental samples originated from soil, marine environments and microbiota associated to mammals (e.g. the human gut microbiome), but rarely employing plant-associated microorganisms.

Here we present examples that highlight the enormous microbial and functional diversity, as well as the biosynthetic potential of plant-associated microbiomes for bioprospecting approaches.

2. Functional and structural insights in plant microbiomes from metagenomics

While the structural diversity of plant microbiomes is well-studied now by amplicon sequencing, it is difficult to find general genetic markers to analyze functional diversity. For this purpose, metagenomic datasets have to be compared and studied in depth. Interestingly, microbiome functions are more similar across different environments than previously thought. For example, Ramírez-Puebla et al. (2013) discussed extensively on similar functional traits in the gut and root microbiome. Based on deeper insights obtained by omics technologies, Mendes and Raaijmakers (2015) recently presented their concept that the structure and function of rhizosphere and gut microbiomes show cross-kingdom similarities. This concept was extended by Berg et al. (2015) to ecological rules. To date only a few studies have deciphered the functional diversity of plant microbiota employing shotgun next generation sequencing approaches (rev. in Knief, 2014). For instance, in depth analysis of the *Sphagnum* moss metagenome revealed high functional diversity within the microbiome and a higher structural diversity as previously detected with other methods (amplicon sequencing or cultivation-dependent methods) (Bragina et al., 2014).

In this section we focus on functional and structural diversity of plant metagenomes as summarized in Table 1, which are important criteria when prospecting for novel bioactive compounds. Based on phylogenetic analysis of plant metagenomic data it was demonstrated that bacterial diversity in higher plants (rhizosphere, phyllosphere, endosphere) is remarkably high, even though it is in general lower than the microbial diversity in the surrounding bulk soil (Delmotte et al., 2009; Bulgarelli et al., 2015). High abundance of bacterial taxa in the rhizosphere or phyllosphere of rice, barley, moss, lettuce and soybean belong predominantly to the phyla *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, *Firmicutes*, and *Acidobacteria*. Less abundant but highly diverse phyla with functionally outstanding properties are also present, for example *Cyanobacteria*, *Deinococcus*, and *Chloroflexi* (Delmotte et al., 2009; van der Lelie et al., 2012; Kröber et al., 2014; Bragina et al., 2014; Bulgarelli et al., 2015). The functional diversity of the aforementioned plant-microbiomes has been explored in relation to the plant compartment. In barley roots and rhizosphere, the authors found significant enrichment of biological functions coding for adhesion, stress response, secretion, host-pathogen, microbe-microbe and phage-microbe interactions, as well as iron mobilization and sugar transport (Bulgarelli et al., 2015). In contrast, phyllosphere bacterial communities in clover, soybean and *Arabidopsis thaliana* plants were characterized by high expression of outer membrane proteins (porins, TonB receptors) and ABC-transport systems for carbohydrates (maltose, glucose, sucrose) and amino acids, underlining the role of the phyllosphere microbiota for carbon utilization on the plant leaves (Delmotte et al., 2009).

Other groups have focused on the investigation of highly specialized microbial communities and their metabolic functions, for example on the distribution and abundance of phototrophic bacteria on the plant phyllosphere, with putative functions for light sensing and utilization (Atamna-Ismaeel et al., 2012a,b). Here the authors employed metagenome data mining to elucidate the relative abundance of rhodopsin-based phototrophs and anoxygenic phototrophs on leaves of different plants (tamarisk, clover, rice, soybean, and *A. thaliana*). Rhodopsin coding sequences (Atamna-Ismaeel et al., 2012b), as well as phototrophy-related genes (*pufM*, *bchY*, *pufL*) (Atamna-Ismaeel et al., 2012a), were used as genetic markers for in silico analysis. Several novel rhodopsin sequences were identified, especially in the tamarisk phyllosphere. These findings suggest the presence of highly diverse and phyllosphere-specific phototrophic species in the studied plant microbiomes.

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