

## FLOWER POWER? THE PLANT MICROBIOME AND HUMAN HEALTH ISSUES

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### SUMMARY

The microbiome is crucial for plant growth and health. Recent studies reveal an unexpected microbial diversity and abundance associated with plants. Plant genotype, soil type, climate, geography as well as pest and pathogens were identified as main drivers of the plant microbiota. The plant-associated microbial diversity seems to be impressive but their dimension is not yet understood. During evolution, microbiomes have secretly co-evolved with their host plants. On the other side, within millennia of domestication, crops underwent traceably many different adaptive trends, allowing rapid speciation and divergence that lead to phenotypic and genotypic distinction to their wild ancestors. Together, domestication and intensive agricultural management shifted the crop microbiota. This resulted in diversity loss, which has consequences for human and *one* health issues. The plant microbiome, which is on one hand specifically adapted to the diverse microhabitats of plants – from the seed to the flower – is on the other hand connected to the whole biosphere. First insights reveal inter-connected microbiomes of plants, e.g. with the built environment, food and humans. These connections need to be better understood for sustainable agriculture as well as plant, human and environmental health and functioning.

### INTRODUCTION

Plants and their associated microbes have been interacting with each other for a long time, forming assemblages of species that is referred to as a holobiont (Vandenkoornhuyse et al., 2016). The plant-associated microbiota has the ability to contribute multiple aspects to the functioning of the plant holobiont, such as (i) germination and growth support, (ii) supply of nutrients and minerals, (iii) resistance against biotic stress factors (pathogen defense), (iv) resistance against abiotic factors, and (v) production of bioactive metabolites involved in multifold interactions (Berg et al., 2017). Plants harbour distinct

habitat-specific microbial signatures, which are shaped by a long list of abiotic (soil type, climate, geography) and biotic factors (plant genotype, pest and pathogens). Whipps et al., (1988) were the first who implemented the microbiome concept for plant-associated microbial communities. They defined “*the microbiome as a characteristic microbial community occupying a reasonably well-defined habitat which has distinct physio-chemical properties. The term thus not only refers to the microorganisms involved but also encompasses their theatre of activity*”.

The rhizosphere, which was introduced for the below-ground, root-associated part of the plant by Lorenz Hiltner already in 1901, is one of the best-studied microbiomes at all (*Phillipot et al.*, 2013). The phyllosphere microbiome colonize all above-ground organs, which are exposed to the air and permanently changing abiotic factors such as ultraviolet (UV) radiation, temperature and water, and a general low nutrient availability (*Remus-Emsermann and Schlechter*, 2018). The phyllosphere can be further subdivided into the caulosphere (stems), phylloplane (leaves), anthosphere (flowers), and carposphere (fruits). Ectophytic microbial communities acting in the interface with soil and air, while endophytic communities represent an intimate core of the plant microbiota and connecting the different plant microhabitats and development stages are of special importance for health issues (*Hardoim et al.*, 2015). A reservoir for plant's endophytes is the rhizosphere,

which represents the below-ground interface with the highly diverse soil microbiota (*Berg et al.*, 2005). The flower and seed microbiome are both understudied microhabitats of the plant. The spermosphere is the zone surrounding seeds where interactions between the soil, microbial communities and germinating seeds take place (*Schiltz et al.*, 2012). This microenvironment links the above and below-ground microbiome of plants.

Despite more than 100 years of research and deep knowledge about single plant microbiomes, less is known about transmission and interactions of the plant microbiomes. Therefore, this review will summarize our work about microbiome internal and external interactions – within the plants themselves and with its environment in context with the state of current knowledge. Moreover, these interactions will be discussed in view of plant and human health issues.

## INTERNAL RELATIONSHIPS: THE MICROBIOME DURING PLANT'S LIFE CYCLE

### **The seed microbiome and germination**

Plant's life cycles are connected with sexual reproduction and characterized by two distinct stages in their life cycle: the gametophyte stage (haploid) and the sporophyte stage (diploid). The haploid gametophyte produces the male and female gametes by mitosis in distinct multicellular structures, after fusion of the diploid zygote develops into the sporophyte. After reaching maturity, the diploid sporophyte produces spores by meiosis, which in turn divide by mitosis to produce the haploid gametophyte. The new gametophyte produces gametes, and the cycle continues. Interestingly, the life cycle of higher

plants is dominated by the sporophyte stage, with the gametophyte borne on the sporophyte while in mosses, the haploid gametophyte is more developed than the sporophyte. For a long time, it was assumed that plants recruit the majority of microorganisms from surrounding soil. Recently it was discovered that all plants transmit a core microbiome from one generation to the other, which is strongly specific for each plant genotype (*Berg and Raaijmakers*, 2018).

Mosses, which were the first land plants and which in the past formed the main vegetation, have a long time of co-evolution with their associated microbiota. This resulted in a highly

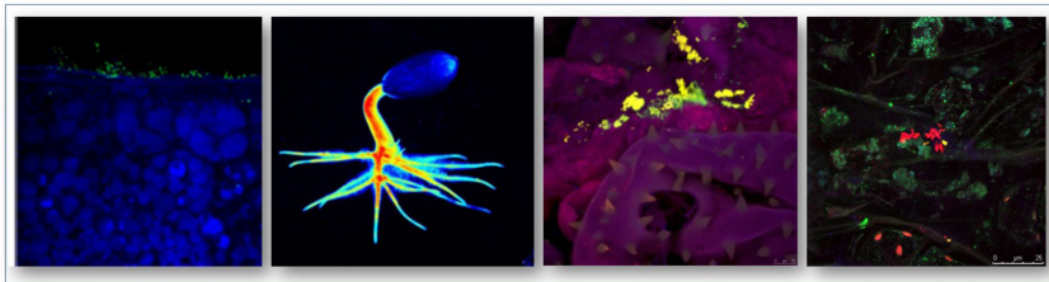
specific and specialized microbiome. For example, *Sphagnum* species have, independently of their origin (Norway, Russia, Germany, Austria) a highly similar microbiome (Opelt et al., 2007; Bragina et al., 2013, 2014). To explain this similarity, the gametophyte as well as the sporophyte was studied. Inside of the sporophyte, a well-defined microbial community was identified, which colonized the gametophyte presenting the moss plant (Bragina et al., 2012). Detailed studies showed that specific microorganisms are essential for their germination procedure (Hornschuh and Kutschera, 2001). Seeds of plants from natural ecosystems are less studied than crop seeds. They have to feature high adaptations in dispersal, persistence and germinative ability under diverse environmental conditions (Fenner and Thompson, 2005). Seeds and seedlings are exposed to a range of hazards like drought, resource limitation, herbivores and eukaryotic or prokaryotic pathogens (Bever et al., 2015). We studied seeds of native alpine plant species growing together for centuries under the same environmental conditions in an Alpine meadow (Hochschwab, Austria). They showed highly unique microbiome signatures and an exceptionally small core microbiome (Wassermann et al., 2019). The seeds harboured a unique composition of bacteria, archaea and fungi in abundances with approximately  $10^{10}$  gene copy numbers per gram seed. The plant genotype was clearly identified as the main driver, while different life styles had less, and seed morphology no significant impact.

There exist a lot of knowledge on seed-borne pathogens as well as international surveillance system (ISTA, International Seed Testing Association, [www.seedtest.org](http://www.seedtest.org)). In the last decade, crop seeds have been studied as source transmitting a plant-specific core

microbiota with neutral or beneficial plant-interaction (Johnston-Monje et al., 2011, 2016; Adam et al., 2016; Glassner et al., 2018; Gloria et al., 2018). All of these studies reveal also an unexpectedly high diversity and abundance of the seed-associated microbiota (Berg and Raijmakers, 2018). They showed up to 20,000 microbial species and up to two billion of bacterial cells in one seed. In general, the seed microbiota consists of bacteria, archaea and fungi. The presented studies focus also on the main drivers of the seed microbiota. Some recent studies on seed-associated microbiomes describe microbial compositions to vary between different geographical sites (Klaedtke et al., 2016), and soil types and microbiomes (Hardoim et al., 2012; Liu et al., 2013). In addition, chemical and microbial seed treatments shaped the microbiota (Mormile, 2016; Rezki et al., 2016). However, a plant genotype and even cultivar specificity of the seed microbiome has been described frequently (Barett et al., 2015; Adam et al., 2016; Rybakova et al., 2017; Wassermann, et al., 2019). Seed endophytes can even be highly conserved across generations of a plant species (Links et al., 2014). Besides the horizontal transfer of microbiota from diverse environmental sources, thus, vertical transfer of microbiota to the next generation via seeds plays a key role in adjusting the seed microbiome (Truyens et al., 2014).

#### **Assembly and stability of the microbiome in mature plants**

Colonization of emerging seedling is controlled by the plant through different strategies, such as the specific profile of root exudates and its immune system (Doornbos et al., 2012; Tuyens et al., 2014; Sánchez-Cañizares et al., 2017). Microorganism's from seeds and soil, both colonize the plant



**Figure 1:** Visualization of bacterial communities in pumpkin microenvironments during its life cycle (seed, seedling, pistil, and petals) by fluorescence *in situ* hybridisation (FISH) in combination with confocal laser scanning microscopy (CLSM) studies

rhizosphere (Adam et al., 2016). From the rhizosphere, only a certain subset of microorganisms is able to invade the endosphere (Berg et al., 2005; Hardoim et al., 2010). Again, plant secondary metabolites and its immune system are the crucial factors for the selection procedure (Huang et al., 2019). In early stages of plant's life cycle, the microbiome is characterized by high diversity and fluctuation. Mature plants are characterized by a very stable microbiome, while in the senescent bacterial phyla which are associated with degradation, the microbiome is more abundant (Smalla et al., 2001). Microbiome stability and equilibriums are essential for plant functioning during the whole life cycle of a plant (Berg et al., 2017).

### The flower microbiome

Interestingly, flowering is a plant stage, which is characterized by a highly specific microbiome, which was highly visible in microbial fingerprints of different plant species (Smalla et al., 2001). The flower is an underexplored microenvironment. Here, we present some data about pumpkin flowers (Lukesch, 2011): petals, pistils and epigynous ovaries of flowers at different maturation stages as well as fruits were analyzed. All parts of the flowers were colonized with bacterial communities at a similar level ( $2.7 \times 10^6$  to  $1.4 \times 10^7$  16S rRNA gene copies  $\text{ng}^{-1}$  DNA).

Generally, flower parts at withered maturation stage showed higher abundances than at flourish or youngest stage. Functional analysis showed that a high proportion of the bacterial community had antagonistic traits to a broad-spectrum of phytopathogens; they belong to the classes Alphaproteobacteria and Gammaproteobacteria and the phylum Firmicutes. Deep sequencing of Gammaproteobacteria-specific amplicons revealed highest relative abundances of Pseudomonadaceae and Enterobacteriaceae. The analyses at species level showed a predominance of *Pseudomonas viridiflava*, one of the key pathogens of Styrian oil pumpkin, in pistils and petals. Our results were confirmed by fluorescence *in situ* hybridisation (FISH) in combination with confocal laser scanning microscopy (CLSM) studies. Using the FISH-CLSM approach, the colonization of pistils and petals by diverse bacterial communities could be detected (Figure 1). The highest bacterial density was found on pollen grains attached to pistils, which gives rise to the assumption that pollen act as a vector for bacteria between pumpkin plants. This study suggests the oil pumpkin flower as an interesting niche for plant-associated bacteria, which should be further considered as reservoir for bio-control agents. It is also in contrast to the general opinion that the mother

plant is highly suggested to be responsible for the recruitment of the seed microbiota (Nelson, 2018). Recent results by Manirajan et al. (2018) confirmed a high microbial diversity influenced by plant species and pollination type associated with pollen. The knowledge about the anthosphere microbiome was even successfully used for manipulation by introducing beneficial bacteria at flowering into progeny seeds (Mitter et al., 2018).

#### **Domestication and biodiversity loss**

Cultivation of crop plants started 13,000 years ago and today's divergence of domesticated plants to their wild ancestors emerged as a consequence of selecting wild plants that were gathered and cultivated by hunter-gatherers in early domestication periods. Domestication have impacted plant microbiome assembly and functions via habitat expansion and via changes in crop management practices, root exudation, root architecture, and plant litter quality (Pérez-Jaramillo et al., 2016). The authors proposed a "back to the roots" framework that comprises the exploration of the microbiome of indigenous plants and their

native habitats for the identification of plant and microbial traits with the ultimate goal to reinstate beneficial associations that may have been undermined during plant domestication. Seeds transmit the footprint of domestication (Berg and Raaijmakers, 2018), and especially their altered morphology over time is therefore frequently studied by archeobotanic and genomic research.

Hence, threats of plant extinction, driven by modern human culture, affect the whole genomic entirety of the holobiont. Studying the impact of domestication on crop seed microbiomes, the seed microbiomes of plant from natural ecosystems are especially of interest, as solely undisturbed environments are appropriate to explain indigenous plant-microbe-interactions.

In conclusion, the plant microbiome is definitely inter-connect during plant's life cycle. Together, domestication and intensive agricultural management shifted the crop microbiota. This resulted in diversity loss, which has consequences for human and one health issues. More research is needed to discover these internal relationships, and use that knowledge for nature conservation and sustainable agriculture.

### **EXTERNAL RELATIONSHIPS: THE PLANT MICROBIOME AND HUMAN HEALTH ISSUES**

#### **The plant - indoor microbiome connection**

The built indoor microbiome has importance for human health because buildings are complex ecosystems that house not only people, but also trillions of microorganisms interacting with each other (Kembel et al., 2012). Residents leave their microbial fingerprint mainly from their skin (Grice and Segre, 2011) but less is known about the transfer from plants. Our hypothesis that indoor plants

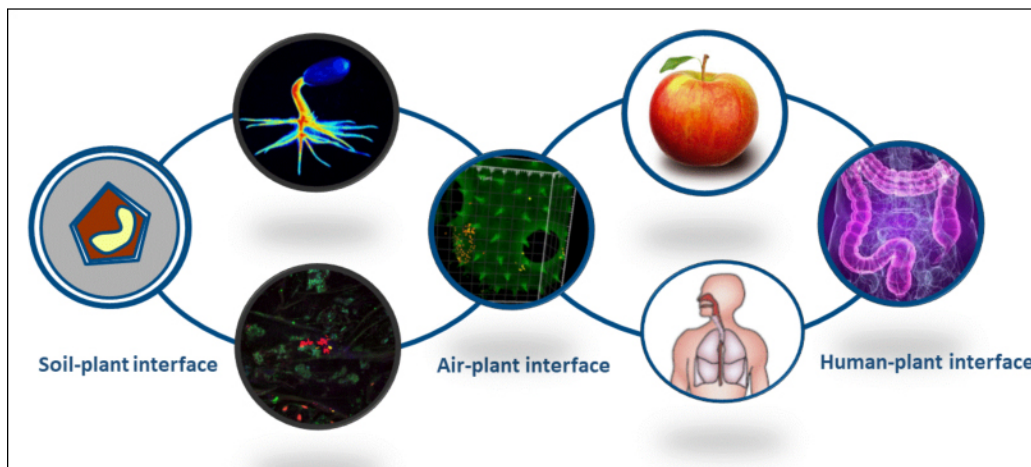
contribute substantially to the microbial abundance and diversity in the built environment was developed after studying the surface microbiome in intensive care units (ICU) of the Graz university hospital (Oberauner et al., 2012). Interestingly, the beneficial part of the ICU microbiome was similar to the phyllosphere microbiome (Berg et al., 2014a). We explained that by window ventilation, and in fact we found evidence for a transfer of pollen and their associated microbiome. The

importance of window ventilation for hospitals was already described by *Kembel et al. (2012)*, who showed that the phylogenetic diversity of airborne bacterial communities was lower indoors than outdoors, and mechanically ventilated rooms contained less diverse microbial communities than did window-ventilated rooms. In a next step, we experimentally confirmed a proof of principle by analyzing the microbiome of the spider plant *Chlorophytum comosum* in relation to their surrounding environment (*Mahnert et al., 2014*). The abundance of Archaea, Bacteria, and Eukaryota (fungi) increased on surrounding floor and wall surfaces within six months of plant isolation in a cleaned indoor environment, whereas the microbial abundance on plant leaves and indoor air remained stable. We observed a microbiome shift: the bacterial diversity on surfaces increased significantly but fungal diversity decreased. The majority of cells were intact at the time of samplings and thus most probably alive including diverse Archaea as yet unknown phyllosphere inhabitants. The next question we had was to which extent plant-specific diversity contribute to the indoor diversity. To understand the microbiota of indoor phyllospheres and its driving factors in built environments, we used an experiment design under controlled conditions by analyzing 14 phylogenetically diverse plant species grown in the greenhouses of the Botanical Garden in Graz (Austria) demonstrating different climate zones (*Ortega et al., 2016; Mahnert et al., 2018*). Statistical analysis showed a significantly higher correlation of community composition - for bacteria as well as for fungi - to plant genotype in comparison to the ambient climatic variables. Finally, we could show that man-made shifts of the microbiome as well as the resistome can be influenced and

compensated by the plant microbiome (*Mahnert et al., 2019*).

### **The food - gut microbiome connection**

Recently, the importance of the plant microbiota for human health was evidenced (*David et al., 2014*). The plant-associated microbial diversity can be transferred to the gut microbiome because fruits and vegetables are the major component of a healthy diet (*Berg et al., 2014b*). One prominent example, which was already studied, are Brassicaceae (*Lebeis, 2015*). All family members are characterized by glucosinolates (GLSs) that are part of the effective defense mechanisms of the plant (*Lüthy and Matile, 1984*). Moreover, *Brassica* species are known for a bacteria-dominated composition of the microbiome and harbour no mycorrhiza. The hydrolysis of GLSs into highly active breakdown products, mostly isothiocyanates (ITC) and nitriles, is caused by myrosinase activity. Those volatile breakdown products are utilized in biofumigation processes, where *Brassica* residues are incorporated into soil as they provide suppressive or control effect against nematodes and soil-borne fungal pathogens like *Verticillium longisporum* (*Witzel et al., 2013*). Interestingly, GLSs are also involved in human health issues; the GLS metabolism has become increasingly important over the past decade due to the exploration of anti-cancer activity of ITCs (*Halkier and Gershenzon, 2006*). Since humans consume their vegetables often cooked, the GLS-metabolizing ability of bacteria (*Tani et al., 1974*) has recently aroused scientific interest. Some authors consider the addition of myrosinase-active bacteria to a *Brassica* rich diet to supplement inactivated plant myrosinases (*Mullaney et al., 2013*). While the majority of bacterial strains known to exhibit myrosinase activity are ubiquitous inhabitants of



**Figure. 2:** Inter-connected microbiomes and their interfaces.

the human intestinal tract (Mullaney et al., 2013), still little is known about myrosinase-active bacteria colonizing edible plants tissues. We showed that due to their GLS content *Brassica* harbour a very specific microbiota containing also myrosinase-active bacteria (Wassermann et al., 2017).

Why is that plant-human microbiome connection so important? The loss of microbial diversity in the gut is associated with acute outbreaks as well as with chronic disease, e.g. allergies, obesity, mental diseases (Turnbaugh et al., 2006). Hanski et al. (2012) found first answers about the global question why biodiversity is so important. They showed a correlation between allergies in children and surrounding microbial biodiversity. Increasing chronic diseases in children were explained by the “missing microbe theory”, which was published by Blaser (2014). In 2017, this was further developed into the “theory of disappearing microbiota and the epidemics of chronic diseases”, which postulate that losses of particular bacterial species of our ancestral microbiota have altered the context in which immunological, metabolic and cognitive development occur in early

life, which results in increased disease. Structural and especially functional microbial diversity is already established as a key factor in preventing human diseases, and is suggested as biomarker for plant health as well (Berg et al., 2017). However, despite many indications, this is not well understood and especially mechanistic studies understanding microbial diversity are missing. To our opinion, to study the plant-human microbiome connection offers an enormous potential to solve human health problems in future.

The microbiome of soil and plants plays a crucial role in plant and ecosystem health (Berg et al., 2017; Laforest-Lapointe et al., 2017). However, overlapping compositions, and interconnected microbiomes of human, animal and plant in connection with health should be considered, and used to expand the version of "One health" that includes environmental health and its relation to human cultures and habits (Flandroy et al., 2018). The inter-linked microbiomes are shown in Figure 2, but the links and transmission routes have to be studied much more in detail.



## CONCLUSIONS

Microbial biodiversity associated with plants is important for plant health; the balance between the microbiota and the host is crucial during the whole life cycle. Diversity loss associated with plants cause plant diseases, outbreaks of human pathogens of plants-origin as well as human health problems. Knowledge on the plant microbiota and their inter-connection can provide solutions to face health problems, e.g. to fight against multi-resistant pathogens and outbreaks. However, it can also

provide solutions for crop production under climate change conditions. Plant microbiome engineering and biotechnology open novel options to develop microbials, which fulfil important functions for the plant host, e.g. nutrient, mineral and vitamin supply, and protection against biotic and abiotic stresses. Altogether, the plant microbiome will be the key to the next green revolution (Science Breakthroughs by 2030; <http://nas-sites.org>).

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