MINIREVIEW

Plant microbial diversity is suggested as the key to future biocontrol and health trends

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One sentence summary: To our opinion, new insights into the plant microbiome have brought about a paradigm shift in our understanding of its role in health and disease and have substantial consequences for biocontrol and health issues.

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ABSTRACT

The microbiome of plants plays a crucial role in both plant and ecosystem health. Rapid advances in multi-omics tools are dramatically increasing access to the plant microbiome and consequently to the identification of its links with diseases and to the control of those diseases. Recent insights reveal a close, often symbiotic relationship between microorganisms and plants. Microorganisms can stimulate germination and plant growth, prevent diseases, and promote stress resistance and general fitness. Plants and their associated microorganisms form a holobiont and have to be considered as co-evolved species assemblages consisting of bacterial, archaeal and diverse eukaryotic species. The beneficial interplay of the host and its microbiome is responsible for maintaining the health of the holobiont, while diseases are often correlated with microbial dysbioses. Microbial diversity was identified as a key factor in preventing diseases and can be implemented as a biomarker in plant protection strategies. Targeted and predictive biocontrol approaches are possible by developing microbiome-based solutions. Moreover, combined breeding and biocontrol strategies maintaining diversity and ecosystem health are required. The analysis of plant microbiome data has brought about a paradigm shift in our understanding of its role in health and disease and has substantial consequences for biocontrol and health issues.

Keywords: plant-associated diversity; plant microbiome; plant pathogens; biocontrol; plant protection; breeding

INTRODUCTION

The plant microbiome has been known to be one of the key determinants of plant health and productivity for more than a century. Lorenz Hiltner began intensive research on this topic as early as 1901 (Hartmann, Rothballer and Schmid 2008). Important discoveries relating to plant-associated microorganisms followed, for example, the rhizosphere effect and the importance of rhizosphere microorganisms in the protection of roots against soil-borne pathogens was discovered (Cook *et al.* 1995; Weller *et al.* 2002) as well as the communication of microorganisms with their plant host (Ryu *et al.* 2003; Hartmann and Schikora 2012). Despite a taxonomic and functional overlap
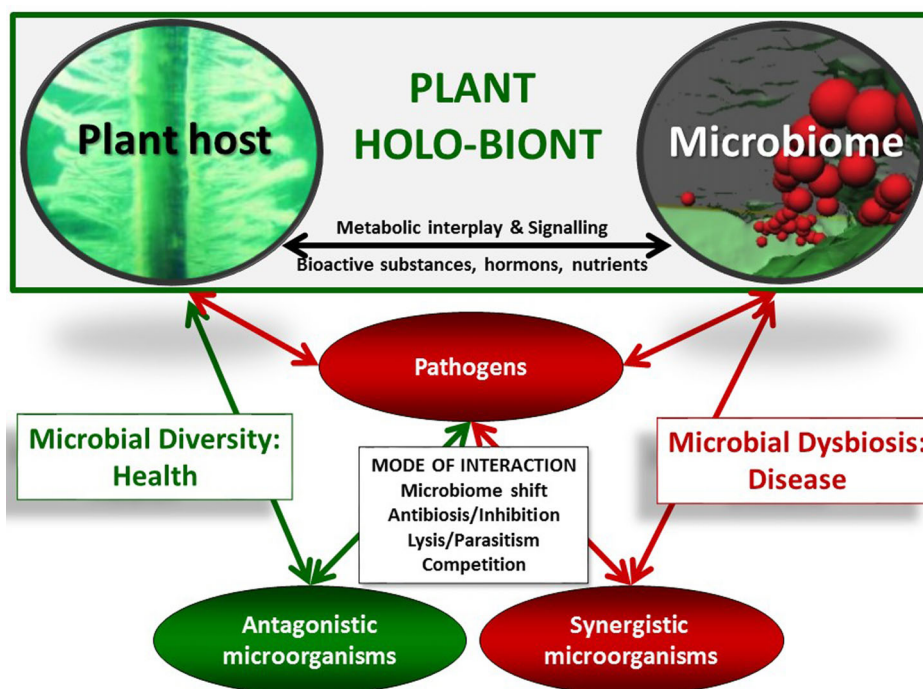
Figure 1. The interplay between the plant and its microbiome in health and disease. Healthy plants are associated with their microorganisms by metabolic co-operation and exchange of signals, hormones and nutrients. Diseases are characterized by a microbial dysbiosis and a response of specific microbes, which can act as antagonists or synergists towards pathogens.

within the plant microbiota (Bai *et al.* 2015), distinct microbiomes were identified for each organ (Vorholt 2012; Philippot *et al.* 2013; Hardoim *et al.* 2015) and plant species (Berg and Smalla 2009). The enrichment of microorganisms by the plant root is not a random, but rather a targeted process. The current model shows the involvement of seed- and soil-borne microorganisms (Adam *et al.* 2016a; Johnston-Monje *et al.* 2016) and the attraction of microbes to roots by nutrients such as carbohydrates and amino acids in combination with plant-specific secondary metabolites (Moe 2013; Weston and Mathesius 2013). Differences in plant root exudates play an important role in the functioning of both chemoattractants and repellents (Badri and Vivanco 2009). Plant defense signaling plays an additional role in these processes (Doornbos, Van Loon and Bakker 2012). Although the structure of plant microbiomes is well studied, there are many knowledge gaps because of the plant species-specific component and because most of the studies were performed on crops and model plants like *Arabidopsis* (Bulgarelli *et al.* 2012). The gaps are especially related to plants in natural ecosystems and their relationship to plant health.

Multi-omics technologies allow much deeper insights into the structure of plant-associated microbial communities, which support and often extend the current body of knowledge (Berg *et al.* 2016; Jansson and Baker 2016). In addition, the tools revealed new functions of the plant microbiome and interactions within the ecosystem. Altogether the plant microbiota has profound effects on soil, plant and agro-ecosystem health (Sessitsch and Mitter 2015). Moreover, the *One* Health and EcoHealth concepts, which emphasize a holistic and interdisciplinary understanding of health, need plant health involvement and strategies, which are just in the beginning stages of investigation (Zinsstag *et al.* 2011). This overview of the state-of-the-art in current literature in addition to own research insights shows that the analysis of plant microbiome data has brought about

a paradigm shift in our understanding of its role in health and disease and has substantial consequences for biocontrol and beyond.

NOVEL INSIGHTS INTO PLANT MICROBIOMES

Plant-associated microbial communities and their functions for plant hosts

Microbial diversity and balance is a key for healthy plants (Yan *et al.* 2017). Traditional knowledge and recent insights form a clearer picture of the functioning of the plant holobiont (Fig. 1). Microbial species have the ability to contribute multiple aspects to the system, including essential functions such as (i) seed germination and growth support through the provision of hormones; (ii) nutrient supply, e.g. by fixation of nitrogen, and the mobilization of phosphorus and minerals such as iron; (iii) resistance against biotic stress factors (pathogen and parasite defense); (iv) resistance against abiotic factors; and (v) physiology and production of bioactive metabolites. In detail, already in the first step of a plant's life cycle, the plant and especially the seed microbiome are crucial for the host (Truyens *et al.* 2015). Seed-associated microorganisms can be essential for the germination procedure in different plant phyla (Hornschuh, Grotha and Kutschera 2006; Alavi *et al.* 2013; Jacquemyn *et al.* 2015; van der Heijden *et al.* 2016). The underlying mechanisms comprise the production of phytohormones, fixation of nitrogen and the mobilization of phosphorus and minerals (Tkacz and Poole 2015). In these cases of germination support, microorganisms are essential, and this may be one reason that these keystone microorganisms are vertically transmitted (Bragina *et al.* 2012; Truyens *et al.* 2015). The plant microbiome is involved in resistance against biotic and abiotic stress factors (Bragina *et al.* 2013). While the mechanisms involved in pathogen defense are well studied
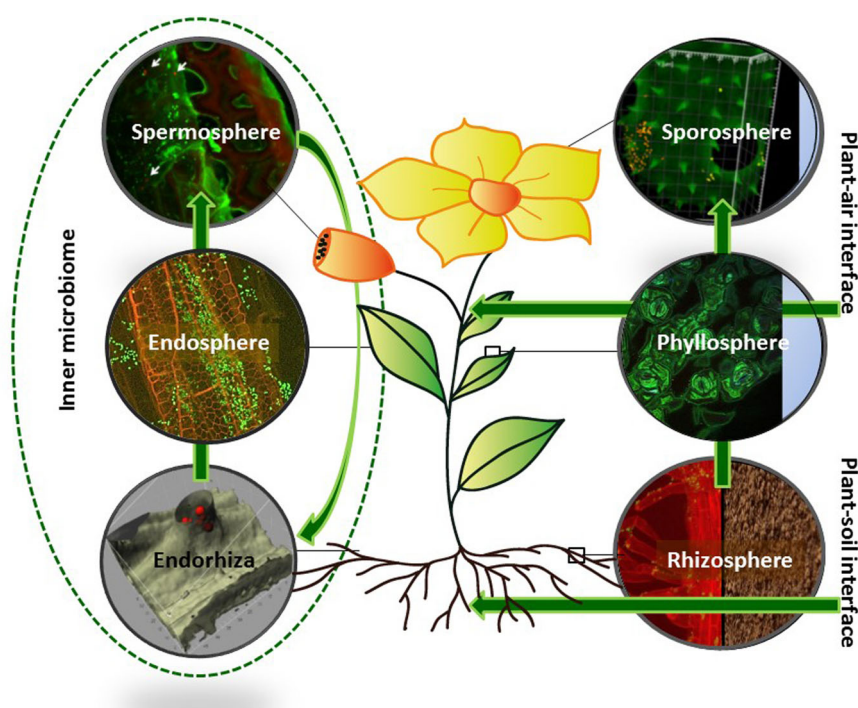
Figure 2. The relationship between plant habitats and their interconnection with the ecosystem.

(Weller *et al.* 2002; Berg 2009; Lugtenberg and Kamilova 2009), the phenomenon of abiotic stress protection, for example, against high salinities and drought, is only at the beginning of the investigations (Yang, Kloepper and Ryu 2009; Zolla *et al.* 2013; Rolli *et al.* 2015). The plant microbiota also has an influence on the physiology and production of bioactive metabolites (Zabetakis, Moutevelis-Minakakis and Gramshaw 1999; Verginer *et al.* 2010). This was also shown for medicinal plants and their active ingredients (Köberl *et al.* 2013b; Schmidt *et al.* 2014). Interestingly, the rhizosphere microbiome was able to be linked to insect feeding behavior, which was most probably a result of microbiome-driven changes in the leaf metabolome of *Arabidopsis* (Badri *et al.* 2013). Peñuelas *et al.* (2014) were able to show that the removal of the floral microbiome of *Sambucus nigra* resulted in a reduced floral terpene emission which plays a key role in pollination and consequently in fruit and seed production. Recent studies also revealed the direct impact of the root microbiome on plant phenology (Wagner *et al.* 2014; Panke-Buisse *et al.* 2015). Additional essential roles of the plant microbiome for phenotypic and epigenetic plasticity as well as the evolution of plants were suggested by Partida-Martínez and Heil (2011) and recently evidenced for mycorrhizal fungi (van der Heijden *et al.* 2016).

Interkingdom signaling and interconnections of the plant microbiome

The cooperation between plants and millions of microbes as well as between them requires an intense communication (Venturi and Keel 2016). A high number of signatures encoding interaction via quorum sensing and other signaling molecules were found in plant-associated microbial metagenomes (Bragina, Berg and Berg 2015); however, the mechanism by which microorganisms interact as a community to confer beneficial traits to plants is still poorly understood. Volatile organic compounds are responsible for 'microbial small talk' but can also act as long-distance messengers for interaction with the

plant host (Schmidt *et al.* 2016). A recent review by Rosier *et al.* (2016) highlights the importance of chemical signaling, and biochemical and genetic events which determine the efficacy of benign microbes in promoting the development of beneficial traits in plants.

Beyond the plant host, the plant microbiome is interconnected with the ecosystem. Although the plant microbiome is divided into specific compartments linked with specific microorganisms, it is also connected with the surrounding environment. The rhizosphere represents the plant–soil interface, from which organic material and signaling compounds migrate into subsoil zones facilitating long-term mineralization processes as part of the biogeochemical and ecological disequilibrium (Berendsen, Pieterse and Bakker 2012; Gocke *et al.* 2017). The phyllosphere and all above-ground organs are connected with the atmosphere and are at the interface for permanent exchange with the air microbiome (Lindow and Brandl 2003). Both ectophytic microhabitats—the phyllosphere and the rhizosphere—present a higher microbial diversity than their endophytic counterparts, the endorhiza and endosphere, because resident and transient microorganisms are co-occurring. Endosphere, carposphere and spermosphere are colonized by specifically adapted microorganisms representing an intimate interaction; they present the internal phytomicrobiome (Fig. 2). The sporosphere included the spores of mosses as well as pollen grains of higher plants, which are morphologically homolog.

The seed microbiome plays a crucial role in a plant's development

The seed microbiome is crucial because it ensures the dissemination and preservation of a co-evolved and specific microbiome to the next generation. In seeds, most of the microorganisms are in a dormant stage and are difficult to isolate (Truyens *et al.* 2015). Through the application of DNA-based techniques, highly diverse seed microbiomes were shown to exist in many plant

species (Adam *et al.* 2016a; Johnston-Monje *et al.* 2016; Klaedtke *et al.* 2016). There are still only a few plant species being analyzed but it seems that seeds transfer a core microbiome to the new plantlets similar to all other organisms including mosses (Bragina *et al.* 2012) and humans (Blaser 2014). However, in textbooks and international trade rules there is evidence that the use of pathogen-free seeds is very important in the production of healthy crops. A large amount of physical and chemical treatments have been developed to obtain pathogen-free seeds. These measures can also lead to the general reduction of microbial diversity and could potentially cause diseases in seedlings due to the fact that beneficial microorganisms supporting germination and growth were also killed. Therefore, we recommend the evaluation of existing methods by omics technologies. We also believe that a combination with biologicals (biopesticides, biostimulants, biofertilizers) can improve the effects of common seed disinfection techniques as suggested by Adam *et al.* (2016b).

The plant microbiome and agriculture

Nearly half of the world's land is used for agriculture according to FAO (Food and Agriculture Organization) statistics. All our crops are 'domesticated' by breeding and man-made evolution. Co-evolution between plants and associated microbial communities, known for wild-type species, has already been hypothesized based on culture-dependent results obtained for the rhizosphere of ancient and modern wheat cultivars (Germida and Siciliano 2001). Co-evolution was recently shown to be prevalent among other plants, e.g. maize, sugar beet, wheat, pumpkin and lettuce, by application of deep sequencing techniques (Peiffer *et al.* 2013; Bulgarelli *et al.* 2015; Cardinale *et al.* 2015; Adam *et al.* 2016a). Crop breeding was identified as strong driver of natural evolution (Berg *et al.* 2013). In some cases, the breeding strategy was targeted at combating pathogens, increasing yield and various growth characteristics, but historically it was a mainly random selection process for plant phenotypes, and changes in the plant microbiome were neglected.

In general terms, most of the management strategies and treatments in agriculture have an impact on microbial diversity and community composition of soils. The concept of the soil memory effect as a potential mechanism for facilitating sustainable plant growth and productivity was recently suggested by Lapsansky *et al.* (2016). Evidence was found in field studies that organically managed crops enrich their own biocontrol potential (Cooper *et al.* 2006; Fließbach *et al.* 2007; Crowder *et al.* 2010; Schmid *et al.* 2011). For example, statistically significant differences in the structure and function of above-ground grapevine-associated microorganisms from organically and conventionally managed vineyards were found in a study by Schmid *et al.* (2011). *Aureobasidium pullulans*, a copper-detoxifying fungus and biocontrol agent, played a key role in explaining these differences.

PLANT PATHOGENS, DISEASE OUTBREAKS AND SUPPRESSIVENESS

What is a plant pathogen?

The presence of microbes in plants became initially noticeable when diseases appeared. However, the vast majority of microbes in plants are not causal agents of damage in plants (Mendes, Garbeva and Raaijmakers 2013). Microbes that are in general able to incite diseases on plant are collectively called plant pathogens. The most common plant diseases are caused by fungi, oomycetes, bacteria, viruses, viroids, virus-like organisms, phytoplasmas, nematodes and parasitic higher plants. In the context of this review, we discuss fungi and bacteria, the largest groups of plant pathogens, as causal agents of plant diseases. A classical definition of plant pathogens assumes that in order to fulfill Koch's postulates, the pathogenic microorganisms must be characterized by pathogenicity/virulence factors. Pathogenicity is defined as the ability of a pathogen to infect and cause disease on a particular host plant, and virulence as a quantitative property is defined as the degree of damage caused to the host (Sacristán and García-Arenal 2008). The degree of a disease is assumed to be negatively correlated with the host fitness (D'Arcy, Eastburn and Schumann 2001). In addition, plant–fungal pathogen interaction can be race-specific and non-specific. Race-specific interaction is known for a large number of leaf pathogens such as rust or powdery mildew fungi (Hovmøller *et al.* 2008), while race-non-specific interaction is described for various soil-borne pathogens. Fungi enter plants through natural openings (e.g. stomata), wounds or by direct penetration of plant tissue. In contrast, bacteria can enter plants only through wounds or natural openings. Diverse pathogens thrive on plant surfaces, while other pathogens inhabit internal plant tissues. Our present knowledge of the factors driving the ecology of plant pathogens is still rather limited as plant pathogens are typically studied mainly on diseased plants. However, there is increasing evidence that members of the microbiome have an important role in the establishment and development of plant diseases (Trivedi *et al.* 2012; Erlacher *et al.* 2014).

Many plant pathogens are either cultivable or diagnostic tools exist for known, not cultivable obligate pathogens. However, despite the substantial progress made in cultivation-dependent methodology (Bai *et al.* 2015), not all microbes retrieved from natural environments are cultivable. Hence, aside from obligate parasites, a lot of pathogens are not cultivable or they might have entered a state called viable but non-cultivable in response to different stresses such as low temperature, salt or UV radiation (Podolich *et al.* 2015). Here, molecular markers and cultivation-independent methods become important for their detection. In addition, there are diseases for which, up until now, no pathogen could be identified or diseases, for which a microbiome imbalance (dysbiosis) of the soil microbiota is likely to play a role, e.g. replant diseases (Mazzola and Manici 2012; Yim *et al.* 2013).

Pathogens can interact with a wide variety of plants independent of the mode of life (biotroph, necrotroph; obligate or facultative). The hosts may range from a few to several hundred plant species. In addition to an endophytic pathogenic lifestyle in a host plant, fungal pathogens can adopt to a contrasting non-pathogenic lifestyle when growing on various other non-host plant species (Freeman, Horowitz and Sharon 2001; Berg, Eberl and Hartmann 2005; Vilhelmsson *et al.* 2016). The fungal plant pathogen *Verticillium dahliae* was identified as a frequent inhabitant of the endosphere in many plants (Götz *et al.* 2006) and used for biological control (Tyvaert *et al.* 2014; Postma and Goossen-van de Geijn 2016). *Rhizoctonia* is another interesting example; it can cause serious symptoms in many crops and has a certain degree of host specificity (Wibberg *et al.* 2015).

Microbial diversity and disease outbreaks

The ubiquitous occurrence of potential pathogens on plants raises the question as to whether the outbreak of certain 'microbiome diseases' is not always dependent on microbial diversity. We know that the resistance of the microbial community to the

invasion of pathogens is linked to its level of diversity (Jousset *et al.* 2011; Van Elsas *et al.* 2012; Mallon, Elsas and Salles 2015) and 'missing microbes' can support disease outbreaks (Blaser 2014). The microbiome of each plant forms a network; these networks can be visualized by co-occurrence patterns (Cardinale *et al.* 2015). The strength and connection of the network is crucial for the invasion success of pathogens and also for the establishment of biocontrol agents. Microbial invasions can cause microbiome shifts, and endophytes can be involved in controlling pathogens in that same manner (Trivedi *et al.* 2012; Erlacher *et al.* 2014; Mercado-Blanco and Lugtenberg 2014; Podolich *et al.* 2015). Mendes *et al.* (2007) observed the suppression of *Fusarium moniliforme* on sugarcane by endophytic isolates of the *Burkholderia cepacia* complex. Microbes can also inhibit the induction of pathogenic genes by impairing them with quorum sensing or otherwise the pathogens have to compete with microbes for plant resources (Friesen *et al.* 2011). In addition, microbes can directly influence plant defense response by producing antagonistic molecules within plant tissue or on the surface of the plants (Fravel 1988). An indirect influence on a plant host's defensive response level is evidenced either as an alteration in defense pathways or as an improvement of plant vigor (e.g. via the production of hormones). We know that microorganisms can support the pathogens (Erlacher *et al.* 2014). These are often members of the *Enterobacteriacea* family, known for their degrading capacity of plant tissues. Both responder groups, those who support and antagonize the pathogen, have to be considered as interesting targets for biocontrol approaches in the development of plant protection methods.

Interestingly, soil microbiota was identified as causal agent of suppressive soils. Historically, crop rotation is one of the oldest plant protection methods as cited in biblical teachings. In recent decades, crop rotations became shorter and in the USA there is a long tradition of monocultures. There is no doubt that crop rotation is a highly efficient method of controlling many diseases, and this can be explained by the great extent of specificity of the plant microbiome, which enhances the overall microbial diversity in soil. A multitude of pathogens existing as normal members of these communities have a low outbreak potential. In monocultures, an increase of pathogen density resulted in severe disease followed by an increase of antagonistic microorganisms which in a best-case scenario cause suppressiveness (Mazzola 2004). This phenomenon was intensively studied in wheat monocultures in the Pacific Northwest (Weller *et al.* 2002) and was recently defined as soil immune response to pathogens (Raaijmakers and Mazzola 2016).

There are important future perspectives for linking plant microbiome and diseases by monitoring. Microbiome-wide association studies in human medicine revealed complex interactions among the microbiome and the environment as first keys for developing precision diagnostics and therapies that are based on the microbiome (Gilbert *et al.* 2016). This can be endorsed as a worthy objective not only for the promotion of plant health but also for the promotion of soil health, which are closely connected.

MICROBIOME-BASED SOLUTIONS FOR PLANT PROTECTION

Microbiome and biocontrol strategies

Plant diseases are the cause of major economic losses for farmers worldwide. The FAO estimated that pests and diseases are responsible for about 25% of crop loss (Martinelli *et al.* 2014).

There are regional differences reported: it is estimated that diseases typically reduce crop yields by 10% every year in more developed settings, but yield loss due to diseases often exceeds 20% in less developed areas. Disease control is reasonably successful for most crops and is achieved by use of plants that have been bred for appropriate resistance against many diseases, by plant cultivation approaches such as crop rotation, use of pathogen-free seeds, appropriate planting date and plant density, and by chemical and biological control. Most of these plant protection methods can influence the plant microbiome and therefore new insights should be taken into consideration for the improvement of plant protection strategies. In many cases, diseases are associated with microbiome imbalances or shifts which makes exploitation of the entire microbiome a desirable objective. Analyzing the plant microbiome as well as the metabolic interplay with the host plant opens new doors for advanced biocontrol technologies (Berg 2015).

New insights reveal an impressive microbial diversity amongst all plants and novel antagonistic microorganisms towards phytopathogens. Despite the fact that plant microbial diversity depends on many factors, there were some facts reported which should be considered in future screening strategies. Mosses, the oldest land plants on Earth, are characterized by a unique microbial diversity (Bragina *et al.* 2012; Bragina, Berg and Berg 2015) and they harbor an extraordinary potential of antagonists due to their ecology (Opelt *et al.* 2007). Furthermore, medicinal plants have been evaluated as being an interesting source for biodiversity (Köberl *et al.* 2013a). This originates from their rich secondary metabolism, which triggers the plant microbiome composition. Endemic plants were also identified as being unique sources for biodiversity and antagonists (Zachow *et al.* 2014). Due to novel insights, we expect that endophytes, and in particular seed endophytes, can serve as sources for novel biocontrol agents. Up to now, mainly bacteria and fungi have been exploited for biocontrol purposes. Archaea were recently identified as plant microbiome members (Müller *et al.* 2015); their functions on plants and their potential for biocontrol are completely unknown.

As mentioned above, all microorganisms associated with plants form a network which can be influenced by microbial invasion. These network models of soil and plant microbiomes provide new opportunities for enhancing disease management and can be deciphered for biocontrol. Poudel *et al.* (2016) suggested a framework for interpreting microbiome networks, illustrating how observed network structures can be used to generate testable hypotheses about candidate microbes affecting plant health. They presented four different types of network analyses: (i) general network analysis to identify candidate taxa for maintaining an existing microbial community, (ii) host-focused analysis to include plant responses, (iii) pathogen-focused analysis to identify taxa with direct or indirect associations with taxa known *a priori* as pathogens and (iv) disease-focused analysis to identify taxa associated with disease. Interestingly, there are a lot of parallels to manage invasive plants by symbiotic microorganisms (Kowalski *et al.* 2015).

Most of the potential biocontrol agents were screened by *in vitro* antagonisms against the pathogen. Despite the fact that many of these screenings yielded in successful biocontrol agents, there is a long and intense debate about this screening assay. One reason is that many of the efficient plant growth promoting and biocontrol organisms *in vivo* show no or only modest *in vitro* antagonisms (Adesina *et al.* 2009; Schreiter *et al.* 2014a). High-throughput *in planta* assays were developed, but they also showed disadvantages because of their artificial

character. For example, treatment of oilseed rape seeds with *Paenibacillus* showed a negative effect on the plant growth under gnotobiotic conditions, no effect in sterile soil, but plant growth promotion in natural soil (Rybakova *et al.* 2016b). Thus, testing of the potential plant growth promoting and biocontrol strains needs to be done in soils and the effects of plant species and soil types need to be tested. Schreiter *et al.* (2014b) could show that similar genera, among them *Pseudomonas*, were enriched in the rhizosphere of lettuce grown under field conditions in three different soil types. This finding might explain that the soil types did neither influence the rhizo-competence nor the biocontrol activity. Recently, microbiome shifts were discussed as potential novel mechanisms for biocontrol (Schmid *et al.* 2011; Grosch *et al.* 2012; Erlacher *et al.* 2014; Schreiter *et al.* 2014a). The potential mechanisms of microbiome shifts are not well studied but it is assumed that they might include several direct interactions with plant pathogens as well as indirect interactions via the plant by stimulation of the plant immune system (Berg 2009; Lugtenberg and Kamilova 2009). *Bacillus amyloliquefaciens* FZB42, which is a commercialized and efficient plant strengthener, is able to enhance overall microbial diversity (Erlacher *et al.* 2014). Targeting enhanced diversity as biomarker for screening methods will be an interesting objective.

The development and application of biological control products is an increasingly attractive objective worldwide. While single organisms were mainly used in the past, often correlated with inconsistent effects, it is now possible to develop microbiome-based biocontrol strategies (Berg *et al.* 2013). Emmert and Handelsman (1999) recommended Gram-positive bacteria as a good potential candidate for biocontrol applications. And indeed, looking on the registered products and those which are in the pipeline, most of the products are based on *Bacillus* (e.g. EU pesticides database). There are mainly technological reasons for the prevalent use of *Bacillus* as a base product: in comparison to Gram-negative bacteria, bacilli are able to develop spores to survive unfavorable conditions. These spores are easy to formulate and have a high shelf life. When we examined the plant-associated microorganisms which comprise thousands of bacterial species, we came to the realization that only a small proportion of their taxonomic diversity is currently being exploited for biocontrol purposes. Moreover, *Firmicutes* (e.g. *Bacillus*) normally present a small proportion of the plant microbiome; Janssen (2006) reported them as being contributors to a mean of only 2% (range 0%–8%) in the total bacterial soil community. Exceptions were published by Köberl *et al.* (2011) who found up to 37% of *Firmicutes* (*Bacillus* and *Paenibacillus*) in soils of arid environments. There is still an ongoing debate regarding the mode of action of *Bacillus* on plants as well as towards plant pathogens, and although induced resistance and plant growth hormones are reported to be involved in plant–microbe interaction, it is clear that all *Bacillus* and *Paenibacillus* strains are able to produce a long list of bioactive substances and antibiotics (Cawoy *et al.* 2015; Rybakova *et al.* 2016a). Due to the fact that *Bacillus* and *Paenibacillus* strains and spores are highly persistent in the environment, a reduction of plant-associated microbial diversity may be an outcome. Therefore, we would again like to emphasize our demand for more diversity among and within biocontrol products. New cultivation strategies should be developed and applied to exploit the entire antagonistic diversity associated with plants (Zachow *et al.* 2013).

Antibiotic resistances are spreading globally, threatening our ability to treat common infectious diseases, resulting in prolonged illness, disability and death. Unfortunately, agricultural practices such as the use of antibiotics in the livestock indus-

try lead to increased levels of resistance (Ferber 2002; Jechalke *et al.* 2014). The spreading of manure can transfer resistances into plant production systems; due to their bioactive secondary metabolites plants often enriched resistant bacteria in their rhizosphere (Berg, Eberl and Hartmann 2005). Although antibiotic resistance is ancient and widespread in environmental bacteria, risk assessment studies to minimize the emergence and impact of resistance for the whole cycles are needed. Although many biocontrol agents showed low persistence on plants and in soil (Scherwinski, Grosch and Berg 2008), the massive application of spore-forming bacteria could change this picture. Moreover, as most soil bacteria, bacterial antagonists in general, and *Paenibacillus* in particular, do not only contain antibiotic production genes but show also high numbers of antibiotic resistance genes resulting from their ecological background and their antagonistic function within the microbiome. The potential mobilization of these resistance genes via different routes of horizontal gene transfer needs further investigation.

Future health trends

Targeted microbiome engineering for crops is a future trend. Biodiversity should be a biomarker for these microbiome modulations. Higher plant-associated diversity can be achieved not only through the implementation of biological control agents which shifts the microbiome (Erlacher *et al.* 2014), but also by the application of microbial consortia. In this context, crop-specific biological consortia can be taken together from a pool of selected biocontrol agents. Unfortunately, the application of several microbial strains for biocontrol reasons is currently limited in the European Union by the necessity of registering each of the strains, which is a very long and expensive process.

David *et al.* (2014) showed that food-borne microbes from diet were able to survive and transiently colonized the gut. The plant-associated microbial diversity can be transferred to the gut microbiome because fruits and vegetables are the major components of a healthy diet. However, outbreaks are due to alterations of the gut microbial diversity and are associated with chronic disease, e.g. allergies, obesity and mental diseases (Gilbert *et al.* 2016). Increasing chronic diseases in children can be explained by the 'missing microbe theory' published by Blaser (2014). Microbial diversity is already established as a key factor in preventing human diseases and should be implemented in plant protection measures.

Concluding remarks

Continued advances in phytopathology and microbial ecology are needed to improve disease control, and to keep pace with changes in disease pressure caused by the ongoing evolution and movement of plant pathogens and changes in agricultural practices. In order to effectively address this issue, all crop plants have to be recognized as holobionts. Plant-associated microbial diversity is a crucial factor for plant health. Although the task remains for us to clarify the question of what specifically constitutes a healthy microbiome, microbial diversity can be used as a biomarker for healthy plant microbiomes, e.g. in breeding and biocontrol strategies. Targeted and predictive biocontrol approaches are possible by taking a holistic approach and integrating microbiome-based solutions. Moreover, combined breeding and biocontrol strategies maintaining diversity and ecosystem health are required. These systemic approaches are required in order to avoid further losses of our biodiversity and to ensure sustainable agricultural practices.

References

Adam E, Bernhart M, Müller H *et al*. The *Cucurbita pepo* seed microbiome: genotype-specific composition and implications for breeding. *Plant Soil* 2016a, DOI: 10.1007/s11104-016-3113-9.

Adam E, Groenenboom AE, Kurm V *et al*. Controlling the microbiome: microhabitat adjustments for successful biocontrol strategies in soil and human gut. *Front Microbiol* 2016b; **7**:1079.

Adesina MF, Grosch R, Lembke A *et al*. *In vitro* antagonists of *Rhizoctonia solani* tested on lettuce: rhizosphere competence, biocontrol efficiency and rhizosphere microbial community response. *FEMS Microbiol Ecol* 2009;**69**:62–74.

Alavi P, Starcher MR, Zachow C *et al*. Root-microbe systems: the effect and mode of interaction of Stress Protecting Agent (SPA) *Stenotrophomonas rhizophila* DSM14405(T.). *Front Plant Sci* 2013;**4**:141.

Badri DV, Vivanco JM. Regulation and function of root exudates. *Plant Cell Environ* 2009;**32**:666–81.

Badri DV, Zolla G, Bakker MG *et al*. Potential impact of soil microbiomes on the leaf metabolome and on herbivore feeding behavior. *New Phytol* 2013;**198**:264–73.

Bai Y, Müller DB, Srinivas G *et al*. Functional overlap of the *Arabidopsis* leaf and root microbiota. *Nature* 2015;**528**:364–9.

Berendsen RL, Pieterse CM, Bakker PA. The rhizosphere microbiome and plant health. *Trends Plant Sci* 2012;**17**:478–86.

Berg G. Plant-microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture. *Appl Microbiol Biot* 2009;**84**:11–8.

Berg G. Beyond borders: investigating microbiome interactivity and diversity for advanced biocontrol technologies. *Microb Biotechnol* 2015;**8**:5–7.

Berg G, Eberl L, Hartmann A. The rhizosphere as a reservoir for opportunistic human pathogenic bacteria. *Environ Microbiol* 2005;**7**:1673–85.

Berg G, Rybakova D, Grube M *et al*. The plant microbiome explored: implications for experimental botany. *J Exp Bot* 2016;**67**:995–1002.

Berg G, Smalla K. Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiol Ecol* 2009;**68**:1–13.

Berg G, Zachow C, Müller H *et al*. Next-generation bio-products sowing the seeds of success for sustainable agriculture. *Agronomy* 2013;**3**:648–56.

Blaser M. *Missing Microbes*. London: Oneworld Publications, 2014.

Bragina A, Berg C, Cardinale M *et al*. *Sphagnum* mosses harbour highly specific bacterial diversity during their whole lifecycle. *ISME J* 2012;**6**:802–13.

Bragina A, Cardinale M, Berg C *et al*. Vertical transmission explains the specific *Burkholderia* pattern in *Sphagnum* mosses at multi-geographic scale. *Front Microbiol* 2013; **4**:394.

Bragina A, Berg C, Berg G. The core microbiome bonds the Alpine bog vegetation to a transkingdom metacommunity. *Mol Ecol* 2015;**24**:4795–807.

Bulgarelli D, Garrido-Oter R, Münch PC *et al*. Structure and function of the bacterial root microbiota in wild and domesticated barley. *Cell Host Microbe* 2015;**17**:392–403.

Bulgarelli D, Rott M, Schlaeppi K *et al*. Revealing structure and assembly cues for *Arabidopsis* root-inhabiting bacterial microbiota. *Nature* 2012;**488**:91–5.

Cardinale M, Grube M, Erlacher A *et al*. Bacterial networks and co-occurrence relationships in the lettuce root microbiota. *Environ Microbiol* 2015;**17**:239–52.

Cawoy H, Debois D, Franzil L *et al*. Lipopeptides as main ingredients for inhibition of fungal phytopathogens by *Bacillus subtilis/amyloliquefaciens*. *Microb Biotechnol* 2015;**8**:281–95.

Cook RJ, Thomashow LS, Weller DM *et al*. Molecular mechanisms of defense by rhizobacteria against root disease. *P Natl Acad Sci USA* 1995;**92**:4197–201.

Cooper JM, Schmidt CS, Wilkinson A *et al*. Effect of organic, 'low-input' and conventional production systems on disease incidence and severity in winter wheat. *Asp Appl Biol* 2006;**80**:121–6.

Crowder DW, Northfield TD, Strand MR *et al*. Organic agriculture promotes evenness and natural pest control. *Nature* 2010;**466**:109–13.

D'Arcy CJ, Eastburn DM, Schumann GL. Illustrated glossary of plant pathology. *Plant Health Instr* 2001, DOI: 10.1094/phi-i-2001-0219-01.

David LA, Maurice CF, Carmody RN *et al*. Diet rapidly and reproducibly alters the human gut microbiome. *Nature* 2014;**505**:559–63.

Doornbos RF, Van Loon LC, Bakker PA. Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere. A review. *Agron Sustain Dev* 2012;**32**:227–43.

Emmert EA, Handelsman J. Biocontrol of plant disease: a (Gram-)positive perspective. *FEMS Microbiol Lett* 1999;**171**:1–9.

Erlacher A, Cardinale M, Grosch R *et al*. The impact of the pathogen *Rhizoctonia solani* and its beneficial counterpart *Bacillus amyloliquefaciens* on the indigenous lettuce microbiome. *Front Microbiol* 2014;**5**:175.

Ferber D. Antibiotic resistance. Livestock feed ban preserves drugs' power. *Science* 2002;**295**:27–8.

Fließbach A, Oberholzer HR, Gunst L *et al*. Soil organic matter and biological soil quality indicators after 21 years of organic and conventional farming. *Agr Ecosyst Environ* 2007; **118**:273–84.

Fravel DR. Role of antibiosis in the biocontrol of plant diseases. *Annu Rev Phytopathol* 1988;**26**:75–91.

Freeman S, Horowitz S, Sharon A. Pathogenic and non-pathogenic lifestyles in *Colletotrichum acutatum* from strawberry and other plants. *Phytopathology* 2001;**91**:986–92.

Friesen ML, Porter SS, Stark SC *et al*. Microbially mediated plant functional traits. *Annu Rev Ecol Evol S* 2011;**42**:23–46.

Germida J, Siciliano S. Taxonomic diversity of bacteria associated with the roots of modern, recent and ancient wheat cultivars. *Biol Fertil Soils* 2001;**33**:410–5.

Gilbert JA, Quinn RA, Debelius J *et al*. Microbiome-wide association studies link dynamic microbial consortia to disease. *Nature* 2016;**535**:94–103.

Gocke MI, Huguet A, Derenne S *et al*. Disentangling interactions between microbial communities and roots in deep subsoil. *Sci Total Environ* 2017;**575**:135–45.

Götz M, Nirenberg H, Krause S *et al*. Fungal endophytes in potato roots studied by traditional isolation and cultivation-independent DNA-based methods. *FEMS Microbiol Ecol* 2006;**58**:404–13.

Grosch R, Dealtry S, Schreiter S *et al*. Biocontrol of *Rhizoctonia solani*: complex interaction of biocontrol strains, pathogen and indigenous microbial community in the rhizosphere of lettuce shown by molecular methods. *Plant Soil* 2012;**361**:343–57.

Hardoim PR, van Overbeek LS, Berg G *et al*. The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiol Mol Biol R* 2015;**79**:293–320.

Hartmann A, Rothballer M, Schmid M. Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. *Plant Soil* 2008;**312**:7–14.

Hartmann A, Schikora A. Quorum sensing of bacteria and trans-kingdom interactions of N-acyl homoserine lactones with eukaryotes. *J Chem Ecol* 2012;**38**:704–13.

Hornschuh M, Grotha R, Kutschera U. Moss-associated methylobacteria as phytosymbionts: an experimental study. *Naturwissenschaften* 2006;**93**:480–6.

Hovmøller MS, Yahyaoui AH, Milus EA *et al*. Rapid global spread of two aggressive strains of a wheat rust fungus. *Mol Ecol* 2008;**17**:3818–26.

Jacquemyn H, Waud M, Merckx VS *et al*. Mycorrhizal diversity, seed germination and long-term changes in population size across nine populations of the terrestrial orchid *Neottia ovata*. *Mol Ecol* 2015;**24**:3269–80.

Janssen PH. Identifying the dominant soil bacterial taxa in libraries of 16S rRNA and 16S rRNA genes. *Appl Environ Microb* 2006;**72**:1719–28.

Jansson JK, Baker ES. A multi-omic future for microbiome studies. *Nat Microbiol* 2016;**26**:16049.

Jechalke S, Heuer H, Siemens J *et al*. Fate and effects of veterinary antibiotics in soil. *Trends Microbiol* 2014;**22**:536–45.

Johnston-Monje D, Lundberg DS, Lazarovits G *et al*. Bacterial populations in juvenile maize rhizospheres originate from both seed and soil. *Plant Soil* 2016;**405**:337–55.

Jousset A, Schulz W, Scheu S *et al*. Intraspecific genotypic richness and relatedness predict the invasibility of microbial communities. *ISME J* 2011;**5**:1108–14.

Klaedtke S, Jacques MA, Raggi L *et al*. Terroir is a key driver of seed-associated microbial assemblages. *Environ Microbiol* 2016;**18**:1792–804.

Köberl M, Müller H, Ramadan EM *et al*. Desert farming benefits from microbial potential in arid soils and promotes diversity and plant health. *PLoS One* 2011;**6**:e24452.

Köberl M, Ramadan EM, Adam M *et al*. *Bacillus* and *Streptomyces* were selected as broad-spectrum antagonists against soilborne pathogens from arid areas in Egypt. *FEMS Microbiol Lett* 2013a;**342**:168–78.

Köberl M, Schmidt R, Ramadan EM *et al*. The microbiome of medicinal plants: diversity and importance for plant growth, quality and health. *Front Microbiol* 2013b;**4**:400.

Kowalski KP, Bacon C, Bickford W *et al*. Advancing the science of microbial symbiosis to support invasive species management: a case study on *Phragmites* in the Great Lakes. *Front Microbiol* 2015;**6**:95.

Lapsansky ER, Milroy AM, Andales MJ *et al*. Soil memory as a potential mechanism for encouraging sustainable plant health and productivity. *Curr Opin Biotechnol* 2016;**38**:137–42.

Lindow SE, Brandl MT. Microbiology of the phyllosphere. *Appl Environ Microb* 2003;**69**:1875–83.

Lugtenberg B, Kamilova F. Plant-growth-promoting rhizobacteria. *Annu Rev Microbiol* 2009;**63**:541–56.

Mallon CA, Elsas JD, Salles JF. Microbial invasions: the process, patterns, and mechanisms. *Trends Microbiol* 2015;**23**:719–29.

Martinelli F, Scalenghe R, Davino S *et al*. Advanced methods of plant disease detection. A review. *Agron Sustain Dev* 2014;**35**:1–25.

Mazzola M. Assessment and management of soil microbial community structure for disease suppression. *Annu Rev Phytopathol* 2004;**42**:35–59.

Mazzola M, Manici LM. Apple replant disease: role of microbial ecology in cause and control. *Annu Rev Phytopathol* 2012;**50**:45–65.

Mendes R, Garbeva P, Raaijmakers JM. The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS Microbiol Rev* 2013;**37**:634–63.

Mendes R, Pizzirani-Kleiner AA, Araujo WL *et al*. Diversity of cultivated endophytic bacteria from sugarcane: genetic and biochemical characterization of *Burkholderia cepacia* complex isolates. *Appl Environ Microb* 2007;**73**:7259–67.

Mercado-Blanco J, Lugtenberg B. Biotechnological applications of bacterial endophytes. *Curr Biotechnol* 2014;**3**:60–75.

Moe LA. Amino acids in the rhizosphere: from plants to microbes. *Am J Bot* 2013;**100**:1692–705.

Müller H, Berg C, Landa BB *et al*. Plant genotype-specific archaeal and bacterial endophytes but similar *Bacillus* antagonists colonize Mediterranean olive trees. *Front Microbiol* 2015;**6**:138.

Opelt K, Chobot V, Hadacek F *et al*. Investigations of the structure and function of bacterial communities associated with *Sphagnum* mosses. *Environ Microbiol* 2007;**9**:2795–809.

Panke-Buisse K, Poole AC, Goodrich JK *et al*. Selection on soil microbiomes reveals reproducible impacts on plant function. *ISME J* 2015;**9**:980–9.

Partida-Martínez LP, Heil M. The microbe-free plant: fact or artifact? *Front Plant Sci* 2011;**2**:100.

Peiffer JA, Spor A, Koren O *et al*. Diversity and heritability of the maize rhizosphere microbiome under field conditions. *P Natl Acad Sci USA* 2013;**110**:6548–53.

Peñuelas J, Farré-Armengol G, Llusia J *et al*. Removal of floral microbiota reduces floral terpene emissions. *Sci Rep* 2014;**4**:6727.

Philippot L, Raaijmakers JM, Lemanceau P *et al*. Going back to the roots: the microbial ecology of the rhizosphere. *Nat Rev Microbiol* 2013;**11**:789–99.

Podolich O, Ardanov P, Zaets I *et al*. Reviving of the endophytic bacterial community as a putative mechanism of plant resistance. *Plant Soil* 2015;**388**:367–77.

Postma J, Goossen-van de Geijn H. Twenty-four years of Dutch Trig® application to control Dutch elm disease. *BioControl* 2016;**61**:305–12.

Poudel R, Jumpponen A, Schlatter DC *et al*. Microbiome networks: a systems framework for identifying candidate

microbial assemblages for disease management. *Phytopathology* 2016;**106**:1083–96.

Raaijmakers JM, Mazzola M. Ecology. Soil immune responses. *Science* 2016;**352**:1392–3.

Rolli E, Marasco R, Vigani G *et al*. Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. *Environ Microbiol* 2015;**17**:316–31.

Rosier A, Bishnoi U, Lakshmanan V *et al*. A perspective on inter-kingdom signaling in plant-beneficial microbe interactions. *Plant Mol Biol* 2016;**90**:537–48.

Rybakova D, Cernava T, Köberl M *et al*. Endophytes-assisted biocontrol: novel insights in ecology and the mode of action of *Paenibacillus*. *Plant Soil* 2016a;**405**:125–40.

Rybakova D, Schmuck M, Wetzlinger U *et al*. Kill or cure? The interaction between endophytic *Paenibacillus* and *Serratia* strains and the host plant is shaped by plant growth conditions. *Plant Soil* 2016b;**405**:65–79.

Ryu CM, Farag MA, Hu CH *et al*. Bacterial volatiles promote growth in *Arabidopsis*. *P Natl Acad Sci USA* 2003;**100**:4927–32.

Sacristán S, García-Arenal F. The evolution of virulence and pathogenicity in plant pathogen populations. *Mol Plant Pathol* 2008;**9**:369–84.

Scherwinski K, Grosch R, Berg G. Effect of bacterial antagonists on lettuce: active biocontrol of *Rhizoctonia solani* and negligible, short-term effects on nontarget microorganisms. *FEMS Microbiol Ecol* 2008;**64**:106–16.

Schmid F, Moser G, Müller H *et al*. Functional and structural microbial diversity in organic and conventional viticulture: organic farming benefits natural biocontrol agents. *Appl Environ Microb* 2011;**77**:2188–91.

Schmidt R, Etalo DW, de Jager V *et al*. Microbial small talk: volatiles in fungal-bacterial interactions. *Front Microbiol* 2016;**6**:1495.

Schmidt R, Köberl M, Mostafa A *et al*. Effects of bacterial inoculants on the indigenous microbiome and secondary metabolites of chamomile plants. *Front Microbiol* 2014;**5**:64.

Schreiter S, Ding GC, Grosch R *et al*. Soil type-dependent effects of a potential biocontrol inoculant on indigenous bacterial communities in the rhizosphere of field-grown lettuce. *FEMS Microbiol Ecol* 2014a;**90**:718–30.

Schreiter S, Ding GC, Heuer H *et al*. Effect of the soil type on the microbiome in the rhizosphere of field-grown lettuce. *Front Microbiol* 2014b;**5**:144.

Sessitsch A, Mitter B. 21st century agriculture: integration of plant microbiomes for improved crop production and food security. *Microb Biotechnol* 2015;**8**:32–3.

Tkacz A, Poole P. Role of root microbiota in plant productivity. *J Exp Bot* 2015;**66**:2167–75.

Trivedi P, He Z, Van Nostrand JD *et al*. Huanglongbing alters the structure and functional diversity of microbial communities associated with citrus rhizosphere. *ISME J* 2012;**6**:363–83.

Truyens S, Weyens N, Cuypers A *et al*. Bacterial seed endophytes: genera, vertical transmission and interaction with plants. *Environ Microbiol Rep* 2015;**7**:40–50.

Tyvaert L, França SC, Debode J *et al*. The endophyte *Verticillium* Vt305 protects cauliflower against *Verticillium* wilt. *J Appl Microbiol* 2014;**116**:1563–71.

Van der Heijden MG, de Bruin S, Luckerhoff L *et al*. A widespread plant-fungal-bacterial symbiosis promotes plant biodiversity, plant nutrition and seedling recruitment. *ISME J* 2016;**10**:389–99.

Van Elsas JD, Chiurazzi M, Mallon CA *et al*. Microbial diversity determines the invasion of soil by a bacterial pathogen. *P Natl Acad Sci USA* 2012;**109**:1159–64.

Venturi V, Keel C. Signaling in the rhizosphere. *Trends Plant Sci* 2016;**21**:187–98.

Verginer M, Siegmund B, Cardinale M *et al*. Monitoring the plant epiphyte *Methylobacterium extorquens* DSM 21961 by real-time PCR and its influence on the strawberry flavor. *FEMS Microbiol Ecol* 2010;**74**:136–45.

Vilhelmsson O, Sigurbjörnsdóttir MA, Grube M *et al*. Are lichens potential natural reservoirs for plant pathogens? *Mol Plant Pathol* 2016;**17**:143–5.

Vorholt JA. Microbial life in the phyllosphere. *Nat Rev Microbiol* 2012;**10**:828–40.

Wagner MR, Lundberg DS, Coleman-Derr D *et al*. Natural soil microbes alter flowering phenology and the intensity of selection on flowering time in a wild *Arabidopsis* relative. *Ecol Lett* 2014;**17**:717–26.

Weller DM, Raaijmakers JM, Gardener BB *et al*. Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annu Rev Phytopathol* 2002;**40**:309–48.

Weston LA, Mathesius U. Flavonoids: their structure, biosynthesis and role in the rhizosphere, including allelopathy. *J Chem Ecol* 2013;**39**:283–97.

Wibberg D, Rupp O, Blom J *et al*. Development of a *Rhizoctonia solani* AG1-IB specific gene model enables comparative genome analyses between phytopathogenic *R. solani* AG1-IA, AG1-IB, AG3 and AG8 isolates. *PLoS One* 2015;**10**:e0144769.

Yan Y, Kuramae EE, de Hollander M *et al*. Functional traits dominate the diversity-related selection of bacterial communities in the rhizosphere. *ISME J* 2017;**11**:56–66.

Yang J, Kloepper JW, Ryu CM. Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant Sci* 2009;**14**:1–4.

Yim B, Smalla K, Winkelmann T. Evaluation of apple replant problems based on different soil disinfection treatments—links to soil microbial community structure? *Plant Soil* 2013;**366**:617–31.

Zabetakis I, Moutevelis-Minakakis P, Gramshaw JW. The role of 2-hydroxypropanal in the biosynthesis of 2,5-dimethyl-4-hydroxy-2H-furan-3-one in strawberry (*Fragaria* × *ananassa*, cv. Elsanta) callus cultures. *Food Chem* 1999;**64**:311–4.

Zachow C, Müller H, Tilcher R *et al*. Catch the best: novel screening strategy to select stress protecting agents for crop plants. *Agronomy* 2013;**3**:794–815.

Zachow C, Müller H, Tilcher R *et al*. Differences between the rhizosphere microbiome of *Beta vulgaris* ssp. *maritima*—ancestor of all beet crops—and modern sugar beets. *Front Microbiol* 2014;**5**:415.

Zinsstag J, Schelling E, Waltner-Toews D *et al*. From "one medicine" to "one health" and systemic approaches to health and well-being. *Prev Vet Med* 2011;**101**:148–56.

Zolla G, Badri DV, Bakker MG *et al*. Soil microbiomes vary in their ability to confer drought tolerance to *Arabidopsis*. *Appl Soil Ecol* 2013;**68**:1–9.