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Teng Yang, Yan Chen, Xing-Xiang Wang & Chuan-Chao Dai

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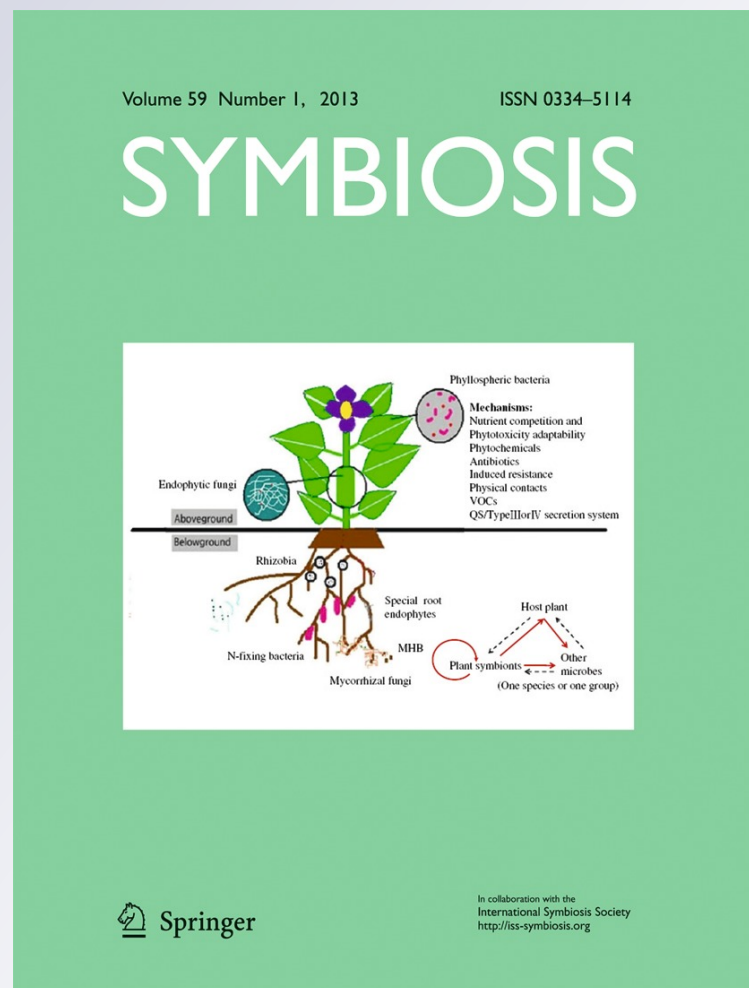
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Plant symbionts: keys to the phytosphere

Teng Yang · Yan Chen · Xing-Xiang Wang · Chuan-Chao Dai

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Abstract The exterior and interior of plants, aboveground and belowground, comprise a complex plant micro-ecosystem, known in recent years as the phytosphere. There are three components: the phyllosphere, endosphere, and rhizosphere. Although in comparison with other ecosystems the phytosphere is small, it similarly includes a great variety of functional microbes. Among these are certain microbes that live in symbiotic relationships with plants; these microbes are known as plant symbionts. Recent research has shown that these symbionts have tremendous effects on plant growth, confer resistance to abiotic stresses and pathogens, aid in the accumulation of metabolites, and have crucial relationships with other plant-associated microbes in the phytosphere. We review the ecological effects of plant symbionts on other microbes, and interactions between plant symbionts in the phytosphere. In addition, we discuss internal mechanisms and suggest future hot spots for research.

Keywords Functional microbes · Phytosphere · Plant symbionts · Ecological effects

Abbreviations

AMF	Arbuscular mycorrhizal fungi
ECMF	Ectomycorrhizal fungi
DSE	Dark septate endophyte
MHB	Mycorrhization helper bacteria
PGPB / PGPR	Plant growth promoting bacteria / plant growth promoting rhizobacteria
P	Phosphorus
N	Nitrogen
K	Potassium
VOCs	Volatile organic compounds
QS	Quorum sensing
TTSS	Type III secretion system
TFSS	Type IV secretion system
AHL	Acyl homoserine lactone

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1 Introduction

Symbiosis is the coexistence of diverse organisms. Over evolutionary time, symbiosis has played a vital role in the formation of highly organized life and new ecological relationships (Shtark et al. 2010). In the early Devonian, the first bryophyte-like land plants had endophytic associations resembling vesicular–arbuscular mycorrhizas (Brundrett 2002). This shows that the evolution of plants from aquatic to terrestrial environments was closely correlated with plant-microbe interactions. Because of the importance of plant-microbe symbioses, researchers have proposed the term “plant symbiont” (Harman 2011).

Microbes that are able to form symbioses with plants without causing obvious symptoms, and confer promotional effects on plant growth, resistance to abiotic and biotic

stresses, or accumulate metabolites, are plant symbionts. They exist in huge variety, and can be divided into two groups: fungal and bacterial. We classify fungal symbionts into three types, as follows: 1. Mycorrhizal fungi (mainly including arbuscular mycorrhizal fungi and ectomycorrhizal fungi); 2. Endophytic fungi (mainly including Type I and Type II endophytes); 3. Special root endophytes (*Piriformospora indica* and various dark septate endophytes) (Table 1). The classification of bacterial symbionts is more complicated. Terms such as ‘plant growth promoting rhizobacteria’ (PGPR) / ‘plant growth promoting bacteria’ (PGPB), ‘mycorrhization helper bacteria’ (MHB), ‘rhizobia’, and ‘N-fixing bacteria’, are used repeatedly in the literature, and all refer to bacterial symbionts. Actually these terms overlap. Figure 1 helps to clarify types of plant bacterial symbionts. The groups PGPB and PGPR contain the majority of plant bacterial symbionts, and we thus use these to describe all plant bacterial symbionts. Five subsets may be identified within PGPB/PGPR, as follows: MHB, legume rhizobia, non-legume rhizobia, N-fixing bacteria (diazotrophic bacteria), and various other plant-associated functional bacteria (Fig. 1). Researchers used to treat rhizobia as a single, special kind of bacterial symbiont, excluded from PGPB (Wang et al. 2012). In this review, we classify rhizobia as a group of PGPB, recognizing that rhizobia are able to significantly promote plant growth.

The phytosphere is an ideal habitat for attracting microbes as it provides sufficient nutrition and a comparatively stable environment (Saito et al. 2007). Microbes, as vital biotic factors in the phytosphere, can transition between trophic states (Kogel et al. 2006; Newton et al. 2010). In addition to plant symbionts there are numerous other plant-associated microbes. These microbes, like the introns of the eukaryotic gene, have no obvious function. However, they are influenced by plant symbionts and may have vital and unknown effects within the phytosphere. It is unfortunate that researchers focus on interactions between plant symbionts and hosts while neglecting the interactions between plant symbionts and other plant-associated microbes. We focus, therefore, on the interactions between plant symbionts and other plant-associated microbes, and the ecological mechanisms of these interactions.

It is well-known that the evolutionary periods of legume–rhizobia symbiosis and AMF–plant symbiosis are quite distinct (60 million years ago and 450 million years ago, respectively) (Bonfante and Genre 2008; Sprent 2008). The plant symbionts described above have differing periods of evolution. In addition, they have different spatial distributions within the phytosphere. Some colonize the rhizosphere, while others colonize the endosphere or phyllosphere (Saito et al. 2007; Compant et al. 2010a; Jansa and Gryndler 2010). Despite their different temporal and spatial scales, two or more different plant symbionts are able to colonize the same plant under natural or artificial conditions. Given the different ecological functions of plant symbionts, researchers hoped to create a single multiple-symbiosis model by which the benefits to the plant could be understood. However, this was on the condition that the ecological functions of the symbionts are not antagonistic towards each other. To what extent does this reflect reality? How is this affected by whether the interactions between plant symbionts are cooperative or competitive? The second focus of this review is thus the interactions between symbionts and their ecological mechanisms.

Two additional points must be clarified. The first is that for plant bacterial symbionts, a single genus or species may have a distinct role in the phytosphere. The genus *Burkholderia*, for example, comprises more than 60 species isolated from a wide range of niches (Suarez-Moreno et al. 2012). In addition to being clinical human pathogens they are plant pathogens, N-fixing bacteria, legume nodulators, and endosymbionts of *Rhizopus microsporus* (Weisskopf et al. 2011; Bontemps et al. 2010; Lackner et al. 2011). “*Candidatus Glomeribacter gigasporarum*”, the endocellular bacterium of *Gigaspora margarita*, also has a close relationship to *Burkholderia* spp. (Bianciotto et al. 2004). These different roles of *Burkholderia* spp. are mainly due to the diversity of plasmidic genetic information within *Burkholderia* spp. A second example is *Rhizobium radiobacter* (formerly *Agrobacterium tumefaciens*); a plant pathogen, plant symbiont of *Sesbania cannabina*, or an endobacterium of *Piriformospora indica* (Wood et al. 2001; Sharma et al. 2008; Cummings et al. 2009). As plant symbiont, *Rhizobium radiobacter* contains no vir genes and lacks tumor-forming

Table 1 Main types of plant fungal symbionts and representative strains

Types of fungal symbiont	Representative strains	Reference
Mycorrhizal fungi	<i>Glomus intraradices</i> , <i>Gigaspora margarita</i> , <i>Laccaria bicolor</i>	Bonfante and Anca 2009; Rigamonte et al. 2010; Ghignone et al. 2012; Bertaux et al. 2005
Endophytic fungi	<i>Neotyphodium</i> / <i>Epichloë</i> , <i>Gilmaniella</i> sp., <i>Phomopsis liquidambari</i> , <i>Curvularia protuberata</i>	Yuan et al. 2010b; Porras-Alfaro and Bayman 2011; Chen et al. 2011; Wang et al. 2011b; Marquez et al. 2007
Special root endophytes	<i>Piriformospora indica</i> , <i>Harpophora oryzae</i> , <i>Phialocephala fortinii</i>	Oelmüller et al. 2009; Sieber 2002; Scervino et al. 2009; Yuan et al. 2010a

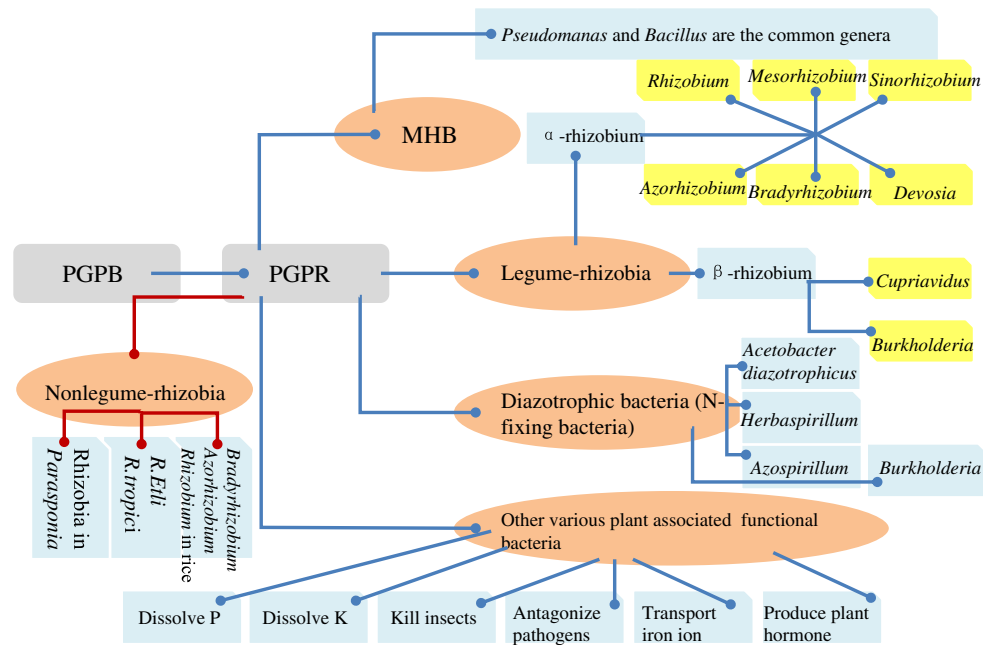


Fig. 1 The classification of various plant bacterial symbionts. The genus *Burkholderia* in β -rhizobia (yellow) includes the following species whose host plants are mainly *Mimosa*: *Bur. tuberum*, *Bur. phymatum*, *Bur. mimosarum*, *Bur. nodosa*, *Bur. sabiae*, *Bur. caribensis*, and *Bur. cepacia*. In addition, *Bur. tuberum* and *Bur. phymatum* are able to fix nitrogen in free living conditions (blue). Another β -rhizobial bacterium, *Cupriavidus*, only comprises one species *Cupriavidus taiwanensis* (syn. *Ralstonia taiwanensis*). Non-legume rhizobia (brown). *Parasponia* is the

ability but harbors a sym-plasmid containing *nifH* and *nodA* genes (Cummings et al. 2009). Whether it behaves as a plant pathogen or symbiont may depend on the plasmid it contains (Zupan et al. 2000; Cummings et al. 2009).

The second point that must be clarified is that for fungal symbionts of plants (*Neotyphodium* / *Epichloë*, *Pi. indica*, *Gigaspora margarita* and *Laccaria bicolor*), and their intimate endo-partners (bacteria or viruses) (Bertaux et al. 2003; Jargeat et al. 2004; Marquez et al. 2007; Sharma et al. 2008; Herrero et al. 2009; Herrero and Zabalgoceazcoa 2011; Petisco et al. 2011). These bacteria and viruses are not by themselves symbionts; however, because of their vital effects on their fungal hosts which are vital to plants, we also regard these bacteria and viruses as plant symbionts.

In short, both the interactions between plant symbionts and other microbes or between different symbionts, are regarded as the interactions of microbes in the phytosphere. Their ecological mechanisms include: competition for nutrition, and a strategy for adapting to phytotoxicity, secretion of antibiotics, production and action of volatile organic compounds, physical contact, induction of plant systemic resistance, and bio-communication systems (Fig. 2). Research and review in these areas will be helpful in explaining and evaluating the ecological effects of plant symbionts, and providing theoretical direction for agricultural applications and ecological protection.

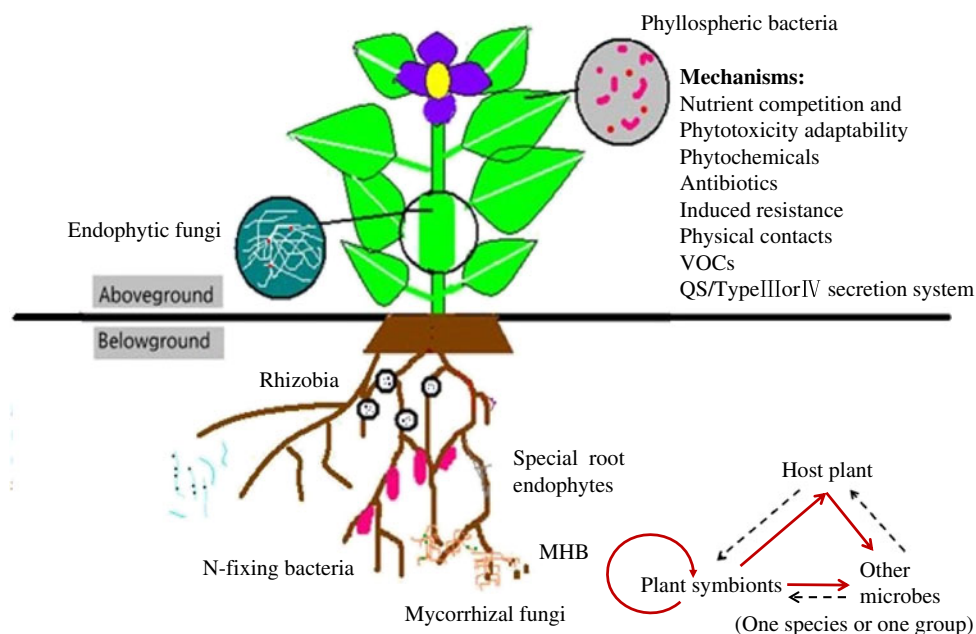
only non-legume genus able to form a *Rhizobium*-like symbiosis. This symbiosis is very similar to the classical *Rhizobium*-legume symbiosis involving biological nitrogen fixation (BNF) and normal nodulation. Second, *Rhizobium etli* and *Rhizobium tropici* are endophytic bacteria of maize. Third, *Bradyrhizobium* spp., *Azorhizobium caulinodans*, and *Rhizobium leguminosarum* bv. *trifolii* are found with rice. They are able to modulate plant root architecture and enhance root hairs but have no BNF or nodulation ability

2 Plant symbionts and phyllospheric microbes

The phyllosphere is a very important bioactive interface between the aerial parts of the plant and the air. It precedes the fixation of carbon dioxide, and the release of molecular oxide, thus facilitating primary productivity. According to a conservative estimate, the phyllospheric area of the world's plants is one billion square kilometers, and is colonized by more than 10^{26} bacteria (Lindow and Brandl 2003). The phyllospheric microbial community has therefore a dominant effect on the global carbon-nitrogen cycle. Plant symbionts appear to be able to modify the phyllospheric microbial community to some degree.

Piriformospora indica was initially isolated from the Thar desert in India, and is an important root symbiont. This fungus has been the subject of a great deal of research owing to the ease with which it may be cultured (Varma et al. 1999; Deshmukh et al. 2006; Camehl and Oelmüller 2010). Although interactions between *Pi. indica* and its host are confined to the rhizosphere, it is interesting that *Pi. indica* is able to use signals which move upward, to confer drought tolerance on Chinese cabbage leaves (Sun et al. 2010). The transmission from roots to aerial plant parts thus allows modulation of leaf pathogens. *Pi. indica* colonization of tomato can limit the leaf disease severity caused by

Fig. 2 Interactions and internal mechanisms among selected plant symbionts, host plants, and associated microbes. The main topics in this review are summarized by the red arrows at lower right



Verticillium dahlia, and decrease the concentration of Pepino mosaic virus in tomato shoots (Fakhro et al. 2010). *Pi. indica* modulates the phyllospheric microbial community through inducing resistance, pH fluctuation, and Ca^{2+} signaling (Vadassery et al. 2009). After *Pi. indica* colonization of *Arabidopsis* it was possible to use jasmonic acid signaling and the cytoplasmic function of NPR1 to induce systemic resistance to the leaf pathogen *Golovinomyces orontii* (Stein et al. 2008). Using noninvasive electrophysiology, researchers found that as soon as *Pi. indica* formed a mutualism with barley, the plant pH changed, and, some days later, plants with *Pi. indica*-colonized roots responded to inoculation of the leaf-pathogenic powdery mildew fungus *Blumeria graminis* f. sp. *hordei* with an apoplastic pH increase in the leaves of about two; significantly different from the control group. Significant changes in leaf apoplastic pH are relevant to the defensive capacity of plants against leaf pathogens (Felle et al. 2009). The effects of fungal symbionts on phyllospheric microbes are not confined to *Pi. indica*. Diverse non-systemic endophytic fungi, defined as type II endophytes, have a wide distribution and modulate phyllospheric microbes, in particular, leaf pathogens (Porrás-Alfaro and Bayman 2011).

Although fungal symbionts occur widely and have widespread effects, most of the pathogens causing great agricultural losses are fungi. The impact of bacteria is minor in comparison. PGPB were able to colonize the rhizosphere, rhizoplane, and inner roots, and even move upward to the aerial parts (Cheng et al. 2010; Compant et al. 2010a). They are able to affect leaf pathogens. The endophytic bacteria *Achromobacter xylosoxidans* and *Bacillus pumilus* are effective against leaf pathogens *Alternaria* sp. and *Verticillium* sp. (Forchetti et al. 2010).

Under poor nitrogen conditions, rhizobia and legumes accrete to form new root organs called ‘nodules’ (Wang et al. 2012). Researchers have found that symbioses between legumes and rhizobia or mycorrhizal fungi may affect the bacterial communities in legume leaves by common signaling pathways (CSPs) or by nodule auto-regulation. In particular, the abundance of Alphaproteobacteria, Gammaproteobacteria, and Firmicutes in phyllospheric microbial communities has been shown to change greatly. Moreover, *Aurantimonas* sp. and *Methylobacterium* sp. have been found to be especially sensitive to nodulation phenotypes (Nishimura et al. 2002; Ikeda et al. 2011). When the same methods were used on the bacterial communities in stems, researchers found that the change in proteobacterial abundance was less than that in the phyllosphere. It was supposed that shoot-derived factor (SDF), for the auto-regulation of nodulation, is produced in the leaves (Sheng and Harper 1997; Ikeda et al. 2010).

Certainly it was clear that native phyllospheric bacterial symbionts were able to affect phyllospheric microbes. Phytochemicals have effects on phyllosphere-colonizing microbes, and the specificity of phytochemicals in different plants creates different dominant bacterial species (Ruppel et al. 2008; Schreiner et al. 2009). Research involving a metaproteogenomic approach to the study of the phyllospheric microbiota associated with the leaves of soybean, clover, and *Arabidopsis thaliana* revealed that *Sphingomonas* and *Methylobacterium* were the predominant phyllospheric members on these three different plant species (Delmotte et al. 2009). Using axenic *Arabidopsis thaliana* and known strains to build a controlled model to study the antagonism of the phyllosphere-dominant bacteria on leaf pathogens *in situ*, has shown that carbon source competition is the

predominant method by which indigenous *Sphingomonas* species antagonize leaf pathogens (Innerebner et al. 2011).

3 Plant symbionts and rhizospheric microbes

The rhizosphere is an intense habitat that includes complex and various root residues and secretions, such as allelochemicals, saccharides, amino acids, and growth factors. These substances play important roles in root elongation and colonization by rhizospheric microbes, and they are often produced by plant symbionts or affected by plant symbionts.

Trichoderma species are avirulent plant symbionts with wide distribution in various ecosystems. Similarly to *Pi. indica*, they are easy to culture *in vitro* (Harman et al. 2004). By mycoparasitism, inducing resistance, producing antibiotics, and competing for ecological niches and nutrition, these plant symbionts have obvious effects on other rhizospheric microbes, particularly pathogens (Brotman et al. 2010). Recent study has shown that although *Fusarium oxysporum* f. sp. *gladioli* produced a secretory toxin, fusaric acid, harmful to *Gladiolus grandiflorus* corms, *Trichoderma harzianum* T-22 was able to decrease the amount of toxin secreted and thus protect the corms (Nosir et al. 2011). Playing the same role as *Trichoderma* species, *Pi. indica* not only suppresses leaf pathogens but also rivals rhizospheric pathogens. When it colonizes barley roots it can urge roots to secrete non-pathogenesis-related proteins to defend against the root rot pathogen *Fusarium graminearum* by inducing systemic resistance. However, this antagonism does not work in pure culture (Deshmukh and Kogel 2007). This suggests that the interaction of *Pi. indica* and *Fus. graminearum* is mediated by the plant. In addition, it is possible that the existence of other microbes in the roots helped the antagonism of *Pi. indica*, bearing in mind the intimate association between *Pi. indica* and several N-fixing bacteria and *Pseudomonas fluorescens* (James and Olivares 1997; Oelmüller et al. 2011).

AMF and rhizobia also have symbiotic relationships with plants, forming mycorrhizae or nodules. Research on Nod and Myc mutant plants showed that although different nodulation phenotypes had little effect on stem bacterial communities, they had significant effects on rhizospheric bacterial and fungal communities. *Pse. fluorescens*, in particular, has been found exclusively associated with Nod⁺ soybean roots. *Fusarium solani* was stably associated with nodulated (Nod⁺ and Nod⁺⁺) roots, and was less abundant in Nod⁻ soybeans. In contrast, basidiomycetes were abundant in Nod⁻ soybeans, and less abundant in nodulated (Nod⁺ and Nod⁺⁺) roots. This suggests that rhizobial symbiosis is able to change the rhizospheric microbial community (Ikeda et al. 2008). Rhizobia, like superstars in a

football team, affect the whole team (the plant) and the other teammates (microbes). Moreover, researchers have found that certain rhizospheric bacteria prefer colonizing mycorrhizal roots. It appears that rhizobia and AMF have certain influences on rhizospheric microbes (Offre et al. 2007). More detailed research found that bacteria in the family Oxalobacteraceae were highly abundant on AMF hyphae (Scheublin et al. 2010). Interestingly, the fungal endophyte *Neotyphodium* which colonizes the aerial tissues of Italian ryegrass, was able to modify host rhizo-deposition, and via this plant-soil feedback, change the soil microbial community (Casas et al. 2011). In addition, the endophyte *Phomopsis liquidambari* was able to express a special enzyme system *in vitro* to optimize the host soil microenvironment, thus effectively changing the number of rhizospheric bacteria, fungi, and actinomycetes, enhancing soil enzyme activity, decreasing pathogen numbers, and degrading phenolic acid (Chen et al. 2010, 2011). These functions may be relevant to the endophytes' expression of saprobic properties *in vitro*, and are distinguishable from the functions of non-endophytic typical saprobes.

4 The interactions of plant symbionts (cooperation or competition)

It is clear that plants are colonized by more than one kind of plant symbiont. Different plant symbionts may use the same symbiotic signals and interact with each other. They either accrete mutually or are antagonistic towards each other. Interactions between different plant symbionts are more complicated than is often thought, and are tripartite: fungi-plant-fungi, fungi-plant-bacteria, bacteria-plant-bacteria, or fungi-plant-virus.

4.1 Fungi-plant-fungi interactions

Symbioses with AMF or DSE are very common in the plant kingdom. However, a recent study observed the co-occurrence of AMF and DSE in seven macrophyte species (De Marins et al. 2009). Furthermore, exudates of a DSE identified as *Dreschlera* sp. stimulated hyphal growth and branching of AMF. However, a negative effect on the extramatrical phase of the AMF was detected (Scervino et al. 2009). The signal transduction mechanisms of these two important fungal symbionts into the roots of host plants, and their effects on the rhizospheric microbial community, are thus interesting and require further study. In addition, when ECMF and AMF colonized *Eucalyptus* at the same time they competed by a nutrition competition strategy (de Boer et al. 2005; Raiesi and Ghollarata 2006). Other research has found that environment, particularly soil moisture, rather than host genetics, had an influence on

colonization by AMF versus ECMF (Gehring et al. 2006). In addition, AMF have complex interactions with endophytic fungi. Considering their independent effects, the joint effects of endophytic fungi and AMF should be even greater. In fact, the increase in plant performance was only found to hold for antagonistic endophytes, while the impact of beneficial endophytes was not altered by AMF infection (Larimer et al. 2010).

4.2 Fungi-plant-bacteria interactions

Fungi-plant-bacteria interactions in the phytosphere have become known from recent studies. The main interactions include ECMF and mycorrhization helper bacteria (MHB), AMF or ECMF, and endobacteria, *Pi. indica* and its endobacterium, or PGPR. Beyond these the most important interaction is among rhizobia, AMF, and leguminous plants.

The role of MHB in the establishment and action of ectomycorrhizal associations has been recently reviewed by Rigamonte et al. (2010), and we will not elaborate. We emphasize, however, that most MHB are PGPR, and *Pseudomonas* and *Bacillus* are the common genera. We presume that not all bacterial species can establish bacteria-fungi-plant interactions. Presumably only special bacteria are able to play key roles in phytospheric ecology.

A new symbiotic model has emerged from one kind of important endobacterium in the spores of AMF *Gigaspora margarita*. From their ribosomal sequences, these bacteria are identified as belonging to a new taxon—“*Candidatus Glomeribacter gigasporarum*”. These bacteria are able to vertically transmit with the sporulation of the host fungus, and they have obligate endocellular properties (Bianciotto et al. 2004). Once the fungi were free from the endobacteria the fungal spores showed certain morphological changes. Moreover, without the endobacteria, the growth and branching of the fungal hyphae were different after treatment with root exudates, suggesting that these special endobacteria have an enormous effect on the symbiosis between AMF and the host plant (Lumini et al. 2007). Using the gene *ftsZ* as the marker of bacterial division, in combination with RT-PCR, researchers have found that when the fungi-plant symbiosis is established, the population of bacteria is the largest and the number of bacteria in AMF ex-root hyphae is larger than in endo-root hyphae (Anca et al. 2009). Strigolactone is a bioactive plant molecule that can stimulate AMF hyphal growth and promote spore germination, even in the absence of the plant. When using this substance to stimulate fungi, researchers found that the number of endobacteria increased. In contrast, when using this plant-derived substance to stimulate endobacteria separated from host fungi, the effect disappeared (Besserer et al. 2006). This suggests the complexity of the fungi-plant-bacteria interaction (Bonfante and Anca 2009), and reveals that endobacteria are

like the mitochondria of fungi. When they are present in the host they can recognize and respond to signals. Once separated from the host they become inactive. Of course, with the growth of AMF, there is increased space and nutrition available for the endobacteria. This may be another key reason for this phenomenon. Recent research concerning the genome of “*Ca. Glomeribacter gigasporarum*” reveals that the endobacteria have an extreme dependence on their host for nutrients and energy, whereas the fungal host is itself an obligate biotroph, relying on the photosynthetic plant. In addition, “*Ca. Glomeribacter gigasporarum*” also expresses type II and type III secretion systems, and synthesizes vitamin B12, antibiotic- and toxin-resistance molecules, which may contribute to the fungal host’s ecological fitness (Ghignone et al. 2012). Similarly ECMF *Laccaria bicolor* was found to have endobacteria related to *Paenibacillus* spp. (Bertaux et al. 2003; Bertaux et al. 2005).

Pi. indica belongs in the order *Sebacinales*; fungi which are extremely versatile in their mycorrhizal associations, and almost universally present as symptomless endophytes (Selosse et al. 2009; Wei et al. 2011). Using quantitative PCR, denaturing gradient gel electrophoresis (DGGE), and fluorescence *in situ* hybridization, researchers detected an intimate association between *Pi. indica* and *Rhizobium radiobacter* (Sharma et al. 2008). They also found that when barley seedlings were dip-inoculated with *Rhizobium radiobacter*, systemic resistance to the powdery mildew fungus *Blumeria graminis* was stimulated. Moreover, through screening additional isolates of the *Sebacina vermifera* complex, three species-specific associations with bacteria from the genera *Paenibacillus*, *Acinetobacter*, and *Rhodococcus* were found. In addition, *Pi. indica* showed an interaction with several nitrogen-fixing bacteria such as *Azospirillum*, *Azotobacter chroococcum*, *Bradyrhizobium*, and *Burkholderia*, resulting in enhanced fungal biomass production (Oelmüller et al. 2011). In contrast, *Pse. fluorescens* significantly suppressed the growth of *Pi. indica*. Co-cultivation experiments with *Pi. indica* showed that *Azotobacter chroococcum* promoted hyphal proliferation whereas *Pse. fluorescens* lysed the hyphae. Other research found that *Pi. indica* was able to promote colonization by PGPR *Pse. striata* on maize and mung beans (Singh et al. 2009). This synergistic action between fungal symbiont and bacterial symbiont on the host plant provided a new way in which plant symbionts worked together to promote plant growth. However, such interactions are not consistent. Investigations of the tripartite interactions among *Paenibacillus lentimorbus*, *Pi. indica*, and *Cicer arietinum* found that number of nodules, dry weight per plant, and N, P, and K uptake by plants were maximum in *Pae. lentimorbus* treatment followed by *Pae. lentimorbus* : *Pi. indica*, and *Pi. indica*, in comparison with a non-inoculated control (Nautiyal et al. 2010). In addition, principal component analysis of carbon source utilization

did not show any clustering among the four samples, suggesting that different combinations of symbionts and plants formed distinct rhizospheric bacterial communities.

Two well-studied examples of major agricultural and ecological importance are the widespread arbuscular mycorrhizal symbiosis and the *Rhizobium*–legume symbiosis. Thirty-two of the 51 studies examining interactions between AMF and rhizobia showed that plants infected with both symbionts had greater plant responses than either symbiont independently or sterile control plants (Larimer et al. 2010). Increased nodule activity and nutrient uptake by plants was found, for example, when plants were symbiotic with both AMF and rhizobia. In addition, colonization by rhizobia was able to stimulate colonization by AMF. Though these two symbioses each have a distinct evolutionary period, they have three vital similarities: 1. The non-legume *Parasponia* rhizobium uses a LysM-Type mycorrhizal receptor to recognize symbiosis signals (Rik et al. 2011). 2. The symbiosis signals of rhizobia have similar structure to the fungal lipochitoooligosaccharide symbiotic signals of arbuscular mycorrhiza (Maillet et al. 2011). 3. The *Rhizobium*–legume symbiosis shares an exocytotic pathway required for arbuscule formation (Ivanov et al. 2012). These three similarities convince us that not only do rhizobia and AMF have an intimate genetic relationship, they also have complex ecological interactions with their plant hosts.

There are other poorly understood and complex tripartite interactions among fungi, plants, and bacteria. *Fusarium oxysporum*, for example, was isolated from an Italian soil that suppresses *Fusarium* wilt (Aloi et al. 1994). Research found that the wild type strain lives in association with a consortium of bacteria belonging to the genera *Serratia*, *Achromobacter*, *Bacillus*, and *Stenotrophomonas*. In addition, small volatile organic compounds (VOCs) emitted from the WT strain negatively influenced mycelial growth in different form species of *Fus. oxysporum*, and repressed expression of two putative virulence genes in a strain of *Fus. oxysporum lactucae*. However, when the WT strain was cured of bacterial symbionts it became a cured form (CU strain) which was pathogenic; causing wilt symptoms. The VOC profiles of WT and CU fungi show different composition, and use of the bacterial VOC had no effect on the growth of the different form species of *Fus. oxysporum* examined (Minerdi et al. 2009). Further research found that the WT strain promoted lettuce growth and expansin A5 gene expression through microbial VOC emissions. β -caryophyllene was found to be the main component of the volatiles released by the WT strain responsible for the plant growth promotion effect (Minerdi et al. 2011). Conversely, the rice pathogenic fungus *Rhizopus* is pathogenic owing to the internal presence of *Burkholderia* strains (Partida-Martinez and Hertweck 2005). These phenomena show the variability and complexity of the role of accompanying bacteria or endobacteria in tripartite interactions.

4.3 Bacteria-plant-bacteria interactions

Legume rhizobia exist in legume rhizospheres. Their persistence in the soil and their colonization of hosts of rhizobia have been found to be affected by soil environment and plant secretions (Wang et al. 2012). The quorum sensing signals of rhizobia were found to be mimicked by plant secretions (Bauer and Teplitski 2001; Fray 2002). In most advanced legume plants, rhizobia were able to pass through infection threads originating from root hairs, and reach nodule primordium cells formed from re-programmed root cortical cells. There, the bacteria were released from the infection threads into the developing nodule cells (Oldroyd et al. 2011). Legume rhizobia include two classes: α -rhizobia and β -rhizobia (Bontemps et al. 2010). Previous research has found that different legume crops, such as soybean (*Glycine max*), alfalfa (*Medicago sativa*), bean (*Phaseolus vulgaris*), and clover (*Trifolium* spp.), have their own special dominant α -rhizobia. Different α -rhizobia were found to compete with each other, and the results of competition depend on their ability to complete infection events in a timely manner and compatibility between host and rhizobia (Graham 2008). With developing research on β -rhizobia, *Burkholderia* spp. have been found to be the most competitive symbionts of *Mimosa*. Three α -rhizobia (*Rhizobium etli*, and two strains of *Rhizobium tropici*) and two β -rhizobial symbionts (*Burkholderia mimosarum* and *Cupriavidus taiwanensis*) were inoculated into three invasive *Mimosa* species for competition studies (Elliott et al. 2009). Under flooded conditions, *Bur. mimosarum* out-competed *Cu. taiwanensis* and the other three α -rhizobia. This was independent of initial inoculum levels, rates of bacterial growth, rhizobia-rhizobia growth inhibition, and individual nodulation rate. Rather, it was determined by environmental N level. Other interesting research has been carried out investigating the relationship between PGPR *Chryseobacterium balustinum* and legume rhizobia (*Rhizobium tropici*, *Rhizobium etli*, *Ensifer fredii*). A co-inoculation assay demonstrated the lack of mutual incompatibility between rhizobial strains and *Chr. Balustinum* (Albareda et al. 2006). The presence of PGPR *Chr. balustinum* was found to affect the rhizobial capacity to attach to soybean roots.

4.4 Fungi-plant-virus interactions

Recently, as research into grass endophytes has developed, researchers have found that mycoviruses are common among different species of endophytic fungi (Herrero et al. 2009). These fungal symbionts are able to inhabit soil and antagonize invertebrate plant pests (Herrero and Zabalgoizecoa 2011; Petisco et al. 2011). However, the ecological functions of these mycoviruses are seldom known. The only one which

is clear is that mycoviruses in the grass endophyte *Curvularia protuberata* are able to confer thermal tolerance on their plant host, a tropical panic grass (Marquez et al. 2007).

5 Mechanisms of ecological interactions concerning plant symbionts

The ecological interactions of plant symbionts are complex and mechanisms consequently vary, but are mainly encompassed by the six points discussed below. These interaction mechanisms are not single; most models involve multiple mechanisms, manifesting in synergistic effects. *Serratia phymuthica*, for example, is an antagonistic rhizosphere bacterium able to suppress symptoms caused by soil-borne pathogens and stimulate plant growth (Kalbe et al. 1996). This bacterial symbiont emits a broad spectrum of volatile organic compounds (VOCs) that are involved in antifungal activity. GS-MS analyses found that WT strains and AHL-negative mutants emitted distinct patterns of volatile organic substances, and this difference in VOCs influenced inhibitory effects on the pathogens *Rhizoctonia solani* and *Verticillium dahlia* (Muller et al. 2009). Actually, except for synergistic effects between quorum sensing (QS) and VOCs, QS acts together with induction of plant systemic resistance (Schuhegger et al. 2006), or with antibiotic production (Liu et al. 2007).

5.1 Nutritional competition and adaptability to phytotoxicity

The phytosphere is rich in nutrition. Some bacteria such as *Pse. fluorescens* have magnanimous siderophores, conferring competitive advantage, occupying ecological niches and being antagonistic towards other microbes. In addition, AMF compete with other soil bacteria for available P in the soil, and when AMF and ECMF colonize *Eucalyptus* they compete within the same ecological niche (de Boer et al. 2005; Raiesi and Ghollarata 2006). Interestingly “*Ca. Glomeribacter gigasporarum*” has an extreme dependence on its host for nutrients and energy, whereas the fungal host itself is an obligate biotroph that relies on the photosynthetic plant. This interphyletic network of nutritional interactions is receiving increasing attention (Ghignone et al. 2012).

Many plants also produce and secrete phytotoxic compounds to inhibit bacterial growth. Bacterial symbionts of these plants have evolved corresponding mechanisms to overcome these. *Rhizobium etli* which normally forms nitrogen-fixing nodules on *Phaseolus vulgaris*, is a natural maize endophyte (Gutierrez-Zamora and Martinez Romero 2001). Several *Rhizobium etli* types were preferentially encountered as putative maize endophytes, because they were most tolerant of 6-methoxy-2-benzoxazolinone (MBOA), a

maize antimicrobial compound that is inhibitory to some bacteria and fungi. This means that the host plant is able to select microbial partners from the environment, and that the right plant symbiont can survive and develop through its adaptation to phytotoxic compounds. Similarly *Rhizobium tropici* was shown to be a competitive maize endophyte owing to its adaptation to phytotoxicity (Rosenblueth and Martinez-Romero 2004).

5.2 Secretion of antibiotics

Environmental microbes, particularly soil and phytosphere-associated microbes, are the main sources of antibiotics. Mycorrhizal fungi can secrete antibiotics to select for resistant bacteria in the mycorrhizosphere and suppress pathogens. In addition, research has shown that some fungal secretory enzymes and bacteria producing antibiotics take action together to suppress pathogens (Woo et al. 2002).

5.3 Production and action of volatile organic compounds

Recent data have shown that many species of below-ground microbes are able to produce VOCs important for microbial communication (Blom et al. 2011). PGPR *Arthrobacter agilis*, isolated from the maize rhizosphere, was able to promote growth and development of *Medicago sativa* seedlings. As part of this process, VOCs as novel signaling molecules are potentially involved in plant-rhizobacterial interactions and are recognized by legumes to modulate root development (Velázquez-Becerra et al. 2011). In addition, VOCs produced by rhizobacteria are involved in interactions with pathogenic fungi as well as with host plants (Kai et al. 2007; Vespermann et al. 2007). Similarly, *Muscodor yucatanensis*, a tropical endophytic fungus from *Bursera simaruba*, produces a complex mixture of VOCs which have a strong allelochemical effects against other endophytic fungi, phytopathogenic fungi, fungoids, and plants (Macías-Rubalcava et al. 2010). The pathogenicity of *Fusarium oxysporum* and its relationship with accompanying bacteria were both found to be associated with VOCs (Minerdi et al. 2009; Minerdi et al. 2011). Interestingly, VOCs produced by rhizospheric strains of *Pse. fluorescens* and *Serratia plymuthica* seem to have another important effect—quorum sensing (QS) quenching. They were able to inhibit the cell-to-cell communicative QS network of various bacteria in the rhizosphere, such as *Agrobacterium*, *Chromobacterium*, *Pectobacterium*, and *Pseudomonas* (Chernin et al. 2011). Through the QS quenching effect by VOCs, certain rhizospheric plant symbionts (a minority) may change other rhizospheric bacterial populations (the majority) which have QS.

5.4 Physical contact

Trichoderma species are powerful mycoparasitic fungi. Because of chemotaxis, they grow toward plant pathogens. Once they contact the host fungus they will twist or grow along the host's hyphae. They will then form hooked structures and secrete extracellular hydrolase to break the host's cell walls, penetrating the hyphae (Viterbo and Horwitz 2010). Furthermore, during mycoparasitic attack, *Trichoderma* species can regulate differential orthologous chitinase genes to coordinate with the physical contact (Gruber et al. 2011). In addition, *Pythium oligandrum* can coil around *Phytophthora infestans* hyphae and parasitize them (Horner et al. 2012). The omnivorous and cosmopolitan plant pathogen *Sclerotinia sclerotiorum* can be infected by the mycoparasite *Coniothyrium minitans* (Huang et al. 2011).

5.5 Induction of plant systemic resistance

Plants evolve a series of defensive mechanisms to protect themselves from various pathogens and pests. Specific pathogen recognition mechanisms are controlled by defense genes. These are stimulated by avirulent symbionts and once pathogens infect there will be hypersensitivity to suppress the pathogens and protect the host plant (Maleck and Dietrich 1999). This often involves plant cell wall solidification, synthesis of phytoalexins, and accumulation of pathogenesis-related proteins (PRs). The stimulation of the plant defense genes means that the effects spread to the whole plant, forming resistance within uninfected and distant tissues. This is called systemic acquired resistance (SAR), and salicylic acid is an important signaling component (Pieterse and Van Loon 1999). Recent research has clearly shown that plant growth regulatory factors, jasmonic acid, ethylene, and epibrassinolide play important roles in the stimulation of plant resistance (Bhardwaj et al. 2010). Exogenously adding the above substances can induce the production of plant defensins and thionin. In addition, endophytic fungi and their elicitors can establish interactions with plants through NO, H₂O₂, salicylic acid, and jasmonic acid (Wang et al. 2011b; Ren and Dai 2012). Once plant defense responses are stimulated, downstream products may affect phytosphere-associated microbes. Non-pathogenic rhizobacteria can also stimulate systemic defensive responses; this is called induced systemic resistance (ISR). This does not require PR protein, but requires ethylene and jasmonic acid (Mur et al. 1997). Whatever is required as the main signaling molecule, the plant symbiont can affect other functional microbes through stimulating defense responses.

5.6 Bio-communication systems among species and kingdoms in the phytosphere: Quorum sensing (QS), the Type III secretion system (TTSS) and the Type IV secretion system (TFSS)

Bacteria, fungi, and host plants occupy different kingdoms. The ecological balance of various prokaryotes and eukaryotes in the phytosphere requires a powerful bio-communication network across species or kingdoms (Witzany 2010). Quorum sensing, the Type III secretion system, and the Type IV secretion system are the main communication modes. In order to transmit messages, bacteria secrete amino acids, oligopeptides, and fatty acid derivatives. These are the “communication languages” that are recognized by autoallergic bacteria or other microbes. Environmental microbes recognize the phytospheric bacterial community and make the corresponding modulations according to the species and concentrations of the signals (Miller and Bassler 2001). The initial description of QS is relevant to symbiosis (Stevens and Greenberg 1997). Later researchers have found that plant symbionts such as rhizobia and *Burkholderia graminis*, or plant pathogens such as *Pse. aeruginosa*, *Rhizobium radiobacter*, and *Erwinia carotovora*, all have QS (Rodelas et al. 1999; Barriuso et al. 2008; Suarez-Moreno et al. 2012). Interestingly, the soil anoxygenic phototrophic bacterium *Rhodospseudomonas palustris* can use *p*-coumarate, a major aromatic monomer of lignin polymers, and acyl-homoserine (acyl-HSL), to produce *p*-coumaroyl-HSL as a QS signal (Schaefer et al. 2008). Because the production of *p*C-HSL needs *p*-coumarate, this QS signal integrates two distinct cues: sufficiently high bacterial population densities and the availability of a particular exogenous substrate. Hence it has functions within the bacterial population and is also a cross-kingdom signal relevant to the host plant. Recently researchers have found that some root-associated fungi can produce special enzymes to degrade acyl homoserine lactone (AHL) *in vitro* (Uroz and Heinonsalo 2008). The importance of the AHL-degrading capacity for the antagonism of mycorrhizal fungi towards pathogens, and the relationships between mycorrhizal fungi and their accompanying bacteria or endobacteria, need further research. In addition, many symbionts such as rhizobia rely on TTSS to communicate (Marie et al. 2001). TTSS and its effectors may create a specific approach in which bacteria and fungi become associated in the phytosphere. The AMF-specific endobacterium “*Ca. Glomeribacter gigasporarum*”, for example, prefers expressing TTSS when the fungus colonizes the host plant (Bonfante and Anca 2009). In addition, TFSS as another important interplay style between bacteria and eukaryotic cells, is present in certain bacteria such as the plant pathogen *Rhizobium radiobacter*, which is also the endobacterium of *Pi. indica* (Sharma et al. 2008).

6 Conclusion and future perspectives

In the phytosphere, the effects of plant symbionts on associated microbes require two main research approaches. One is based on investigation of the phytospheric microbial community, using culture-dependent and culture-independent approaches to study the effects of plant symbionts on the rhizosphere, phyllosphere, and stem bacterial or fungal community structures. This approach amasses a great volume of data and the analytical mechanisms are a little crude. The second approach involves using axenic seedlings or fungicides to create known conditions to study the effect of certain symbionts on single or multiple known bacteria. We call this the “bottle experiment” approach. This approach is able to deeply investigate mechanisms at the levels of proteins and genes. It is possible to integrate the above two approaches: first by conducting total community research and then by using the strain materials and results from microbial community investigation to design a controlled experiment. The integration is likely to provide more dependable and deep results.

In terms of technology and methods, previously widely used methods such as denaturing gradient gel electrophoresis (DGGE), the 16S rDNA gene library, Biolog microplating, and phospholipid fatty acid (PLFA) analysis, are undergoing revolutionary changes. Proteomics now plays a positive role in large-scale microbial community investigation, and also in “bottle experiments”, and shows great investigative power (Marra et al. 2006; Cheng et al. 2010; Wang et al. 2011a; Wu et al. 2011). In addition, the combination of RNA fingerprinting and DNA-stable isotope probing replaces conservative molecular methods at the DNA level, and various functional gene analyses replace analyses based on conservative gene sequencing (16S rDNA or 18S rDNA) (Saito et al. 2007; Ying et al. 2010; Li et al. 2011). In particular, with the further development of ‘omics’ and functional gene microarrays, it will be possible in the future to provide large-scale and holistic information about microbial ecology in the phytosphere very quickly (He et al. 2012; Huang and Zhou 2012). Many unknown mechanisms will be revealed. As Sydney Brenner said, “progress in science depends on new techniques, new discoveries and new ideas, probably in that order”.

With the development of new technology and methodology, research into the effects of plant symbionts on phytosphere-associated microbes is progressing vigorously. In addition, research into the interactions between phytosphere-associated microbes including plant symbionts, and human latent pathogens (Bernier et al. 2003; Grafenhan et al. 2011), the effects of trans-genetic technological applications on agriculture and ecological safety (Barac et al. 2004; Alberghini et al. 2008; Hur et al. 2011; Zhang et al. 2011), and the effects of global climate change on phytosphere-associated microbes

(Antoninka et al. 2009; Compant et al. 2010b; Kivlin et al. 2011) have close relationships with investigations into the mechanisms employed by plant symbionts. Undoubtedly these will be hot spots for future research.

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