REVIEW ARTICLE

BACTERIAL FUNGAL INTERACTIONS – MECHANISMS: A REVIEW

*Rajeshwar Reddy, T. and Prasad, V. R.

Department of Plant pathology, Kerala Agricultural University, India

ARTICLE INFO	ABSTRACT
	Bacterial-fungal interaction (BFIs) means how bacteria initiate and maintain relationship with fungi. The BFIs form physically and metabolically interdependent consortia that harbour properties distinct from those of their single components. The BFIs were mainly associated in two ways namely, ectosymbionts and endosymbionts having either positive or negative interactions. The physical associations and molecular communications lead to alteration in the morphology, reproduction, pathogenecity and symbiosis. Molecular communications of BFIs were mainly through antibiosis, modulation of physiochemical environment, chemo taxis, gene transfer and trophic interactions. The BFIs were excellent model systems, which can be effectively used to understand the fundamental bases of host-pathogen interactions and for identifying different mechanisms of interaction among strains of bacteria and fungi, and also to help design suitable management practices with a broader spectrum of microbial weapons.

INTRODUCTION

Historically, the classical separation of microbiological research between bacteriologists and mycologists has led to the study of bacteria and fungi in axenic settings. This compartmentalization has overlooked the fact that in many environments, bacteria and fungi coexist and interact. Furthermore, these bacterial-fungal interactions (BFIs) often have important ramifications for the biology of the interacting partners. In recent years, research in this area has developed significantly in both breadth and depth. Contemporary studies have revealed that fungi and bacteria often form physically and metabolically interdependent consortia that harbour properties distinct from those of their single components (Tarkka *et al.*, 2009). Bacterial-fungal interaction (BFI) means how bacteria initiate and maintain relationship with fungi. They have considerable ramifications for the biology of the interacting partners. The BFIs form physically and metabolically interdependent consortia that harbour properties distinct from those of their single components (Tarkka *et al.*, 2009). An emerging area of study in the field of host/pathogen interactions involves the relationship established between bacteria and fungi with few exceptions, the majority of characterized bacterial/ fungal interactions (BFIs) are thought to be of little economic importance (Kobayashi and Crouch, 2009). Many BFIs particularly well known for their impact on the environment or human health (Wargo and Hogan, 2006). As a result, BFIs studies and our understanding of these associations have lagged behind similar investigations of

host/pathogen interactions in plant and animal systems. BFIs are becoming known for their importance in human health, agriculture, and the environment and for their potential for advancing discovery in these areas. From an application-based perspective, the parasitism of fungi by bacteria has been used as a tool to provide biological control of plant diseases caused by fungi. BFIs are extremely variable with respect to the impact on the bacterium and fungus. Most common are reports where the bacterial partner exploits resources from the associated fungus through a parasitic or commensality interaction, although there are intriguing examples where the fungus is able to take advantage of bacterial resources in mutualistic interactions (Partida *et al.*, 2007). In this review we described physical and molecular interactions between bacteria and fungi and their role in plant disease management.

Interactions between Bacteria and fungi

Throughout their life cycle, plants and pathogens interact with a wide variety of organisms. These interactions can significantly affect plant health in various ways. In order to understand the mechanisms of biological control, it is helpful to appreciate the different ways that organisms interact. In order to interact, organisms must have some form of direct or indirect contact with each other. Odum (1953) proposed that the interactions of two populations defined by the outcomes for each. The combination of physical associations and molecular interactions between bacteria and fungi can result in a variety of different outcomes for each partner. In turn, these changes may affect the influence of the bacterial-fungal complex.

*Corresponding author: Rajeshwar Reddy,
Department of Plant pathology, Kerala Agricultural University, India

Physical interactions between Bacteria and Fungi

The most intimate BFIs occur when the two partners establish a symbiosis. These symbioses can be classified as either an ectosymbiotic relationship, in which bacteria remain external to the fungal plasma membrane, or endosymbiotic relationship, in which bacteria are located inside the fungal cell. A recently described example of the former is the association of certain *Klebsiella* and *Pantoea* species with the fungal gardens of leaf cutter ants (Pinto-Tomás *et al.*, 2009). Cyanolichens, symbioses formed between fungi (typically ascomycetes, e.g., *Geosiphon pyriformis*) and photosynthetic cyanobacteria (typically belonging to *Nostoc* spp.), are also typically ectosymbiotic (Kluge, 2002). However, a clear example of a cyanolichen endosymbiotic relationship can also be found in the symbiosis between *Geosiphon pyriformis* and *Nostoc punctiforme* (Kluge, 2002). Non photosynthetic endobacteria and ectosymbiotic bacterial partners are also associated with cyanolichens, but their diversity is only beginning to be explored (Bates *et al.*, 2011). While cyanobacteria are intracellular in the association between *Geosiphon pyriformis* and *Nostoc punctiforme*, they are enclosed in a specialized swollen multinucleate fungal "bladder" that is morphologically distinct from the rest of the hyphae, and within this bladder, the cyanobacteria are surrounded by a host-derived symbiosome membrane (Lumini *et al.*, 2006). This arrangement differs from those of other BFIs involving endobacteria, such as those that occur between *Burkholderia* and *Rhizopus* hyphae (Lackner *et al.*, 2009), *Burkholderia* and *Mortierella elongata*, as well as a variety of other endobacteria associated with ecto and arbuscular mycorrhizal fungi (Bertaux *et al.*, 2005). In these pairings, no specialized hyphal structure is present; the bacteria occupy the cytoplasm of hyphae within the fungal mycelium and, in some cases, also fungal spores (Lumini *et al.*, 2006). Indeed, it has been hypothesized that some endobacteria, such as "*Candidatus Glomeribacter gigasporarum*," are obligately dependent on the fungus, as after their isolation from their fungal host, it has not been possible to cultivate them independently in laboratory media (Jargeat *et al.*, 2004). A recent report describing over 400 phylogenetically diverse associations of endophytic bacteria with fungi isolated from foliar tissues indicated that such associations may be far more common than was previously appreciated (Hoffman and Arnold, 2010).

Bacteria that inhabit fungi intracellularly, or endosymbiotically, have been described for more than three decades (Bonfante, 2003). To our knowledge, regardless of their impact of the association with the allied organisms, endosymbiosis is a one-way partnership in that the single-celled bacterium is limited to the role of endosymbiont and the multicellular eukaryotic partner always acts as the host organism as the result of obvious size constraints. (Bianciotto *et al.*, 2001). For endosymbiotic BFIs in the fungal kingdom, however, several factors have contributed to a lack of discovery in the field, including the lack of obvious phenotypes, problems experienced when attempting to establish these organisms in pure culture (Barbieri *et al.*, 2010) and the overall difficulties in establishing experimentally tractable systems. Nonetheless, endosymbiotic BFIs are increasingly gaining recognition for their potential to influence

agricultural systems in a significant manner, and a few model systems are providing insight into their overall lifestyle (Bianciotto *et al.*, 2004). Although the distribution of bacterial endosymbionts includes members of all major classes in the fungal kingdom, mycorrhizal fungi are by far the most common group known to harbor endosymbiotic bacteria. Indeed, the earliest identification of endosymbiotic bacteria was made from cells of the arbuscular endomycorrhizal fungus *Gigaspora margarita*, where it was demonstrated that the endosymbiont was present within vegetative spores, germinating hyphae, and mycelia, even while the fungus was symbiotically associated with a host plant (Bianciotto *et al.*, 1996). Arbuscular endomycorrhizal AM fungi within the family Gigasporaceae, including species of *Gigaspora, Scutellospora, and Gloerella* (Bianciotto *et al.*, 2000) are among the best characterized fungal endosymbiont systems, although bacteria have also been observed in other AM fungi of the Glomeromycota, such as *Glomus versiforme* and *Acaulospora laevis* (Artursson 2005).

Bacterial-Fungal Molecular Interactions and Communication

Interactions via antibiosis

Probably the best-known and most extensively studied category of bacterial-fungal communication is antibiosis, a chemical warfare that is typified by the diffusion of deleterious and often chemically complex molecules from one partner to the other. Research investigating antibiosis has led to the development of numerous important antibiotics to combat microbial infections, the most famous of which is the beta-lactam antibiotic penicillin, which was developed based on the antibiosis of a *Penicillium* mold contaminating a *Staphylococcus* culture (Fleming, 1929). For example, exposure to phenazines and phloroglucinols produced by certain *Pseudomonas* isolates induces the expression of several ABC transporters in the fungal phytopathogen *Botrytis cinerea*, which are thought to prevent the intra hyphal accumulation of antifungal metabolites (Schoonbeek *et al.*, 2007). *B. cinerea* laccase was found to be responsible for the production of reactive species that detoxify 2,4-diacetylphloroglucinol (Schouten *et al.*, 2008). The interaction between the mycorrhizal fungus *Amanita muscaria* and *Streptomyces spp.* strain AcH505 also leads to the suppression of bacterial antibiotic production. In this case, the fungus represses the biosynthesis of the antibiotics WS-5995 B and WS-5995 C by organic acid production (Riedlinger *et al.*, 2006).

Signaling-based interactions

Other molecules have more subtle effects than antibiotics during BFIs by acting as signaling molecules. Some bacterial metabolites stimulate hyphal growth; for instance, during its interaction with *Amanita muscaria, Streptomyces sp.* AcH505 shows an enhanced production of the secondary metabolite auxofuran, which promotes the extension of the fungal mycelium. Unidentified volatile substances produced by some bark beetle-associated bacteria stimulate the growth of their symbiotic fungi (Adams *et al.*, 2009). The reciprocal effect of farnesol and 3-oxo-C12 homoserine lactone is considered due

to the presence of a 12-carbon chain within their chemical structures, since other chemically similar molecules with different carbon chain lengths do not cause similar signaling effects (Hogan *et al.*, 2004). As yet, the role of quorum-sensing signaling in non medical BFIs is largely unexplored, although quorum-sensing systems are present in many environmental bacteria, and there is some evidence that mycorrhizal fungi can degrade quorum-sensing molecules (Uroz and Heinonsalo, 2008). Interestingly, low concentrations of some antibiotics that do not induce bacterial stress responses can have signaling effects on bacterial biofilm formation and motility (Fajardo and Martínez, 2008). This concept has not been extensively studied in the field of BFIs but may be of significant relevance to them, particularly during the early stages of the formation of bacterial-fungal complexes, when antibiotic metabolites may be present in only small quantities (Linares *et al.*, 2006).

Interaction via modulation of the physiochemical environment

Bacterial-fungal communication that is mediated by a specific molecule and a target/receptor, communication in BFIs may occur via modifications of the physiochemical properties of their environment. A common effect is an alteration of the pH, since although some microorganisms (e.g., *streptococci, Lactobacilli*, and *Candida*) can occupy environments under a broad range of pH conditions, most are susceptible to acidic pHs below four (O'May *et al.*, 2005). Similarly, the presence of the alkalinizing yeast *Geotrichum candidum* enhances the growth of *Salmonella* on tomato fruit surfaces (Wade and Beuchat, 2003). The rate of synthesis of the secondary metabolite aflatoxin by *Aspergillus parasiticus* is higher under acidic growth conditions, while alkaline medium increases the production of penicillin by *Aspergillus nidulans* (Calvo *et al.*, 2002).

Interactions via chemotaxis

Diffusible molecules play a significant role in many BFIs, migration and physical contact are also important processes in the establishment of BFIs. Chemotaxis (directed movement) of bacteria toward fungi and fungally derived molecules has been demonstrated in several instances; for example, both detrimental and beneficial *Pseudomonas* species exhibit taxis toward fungal mycelial exudates (Deveau *et al.*, 2010). The molecular nature of bacterial-fungal contact has been examined in only a few systems, and these studies have, perhaps unsurprisingly, highlighted important roles for membrane proteins. For example, the attachment of *Acinetobacter baumannii* to *C. albicans* (Gaddy *et al.*, 2009). Bacterial-fungal contact-based interactions may not be solely adhesive in nature; for example, a lack of O-linked glycans in C. albicans confers hypersensitivity to contact-dependent hyphal death caused by P. aeruginosa (Brand *et al.*, 2008). The main soluble protein found in its fruiting bodies was shown to bind to exopolysaccharides from truffle-associated Rhizobium isolates, suggesting that lectin-mediated interactions may contribute to the selection imposed by the truffle on its associated bacterial community Cerigini (Palla *et al.*, 2006). Trophic interactions Nutritional interactions between fungi and bacteria are important to many BFIs. Trophic competition

between fungi and bacteria is well documented in the plant root environment (rhizosphere), where bacterial competition for nutrients such as carbon nitrogen iron can be an effective biocontrol mechanism against fungal root pathogens. (Elad and Baker, 1985). Examples of bacterial-fungal trophic competition in other environments include competition for carbon substrates during the decomposition of leaves (Moller *et al.*, 1999). Some evidence even suggests an enhancement of cyanobacterial photosynthesis when it is engaged in the symbiosis (Bilger *et al.*, 1994). Nitrogen-fixing bacteria have also been isolated from mycorrhizal (including truffle) fungi and in the fungus gardens of leaf cutter ants, further suggesting positive inputs of endobacteria to fungal nutrition (Pinto-Tomás *et al.*, 2009).

Consequences of Bacterial-Fungal Interactions for Participating Organisms

The successful establishment of an association between bacteria and fungi has profound consequences for both organisms; describe the main outcomes of BFIs in relation to changes in the bacterial and fungal partners physiology, life cycles, and survival. Extracellular bacteria can affect fungal development and spore production, to the benefit or the detriment of the fungus. Bacteria stimulate spore germination in several fungi, including the plant-pathogenic oomycete *Phytophthora alni* (Chandelier *et al* 2006). Another notable effect on fungal development is seen in the life cycle of the edible button mushroom Agaricus bisporus. The commercial production of mushrooms occurs via the initial colonization of mushroom compost by the fungal mycelium followed by casing with a layer of a peat/limestone mix that stimulates fruiting body initiation (Noble *et al.*, 2003)

Effects on bacterial and fungal physiology

Observation of the effects of fungi on bacterial development is difficult due to the small size and single-cell nature of prokaryotes. However, if we consider bacterial-fungal biofilms, it is clear that fungi can promote distinct differences in bacterial development by contributing to a distinctive ecological niche, within which bacteria exhibit physiological differences, such as resistance to antibiotics, stress, and an altered expression of virulence genes, compared to free-living bacteria (Harriott and Noverr, 2010). Fungi and bacteria also play important roles in promoting the survival of their interacting partners. This effect can be reciprocal; for example, *P. fluorescens* BBc6R8 promotes the viability of the mycorrhizal fungus *Laccaria bicolor* under unfavorable growth conditions in soil (Brule *et al.*, 2001), while the fungus can also promote the survival of the bacterium (Deveau *et al.*, 2010). Filamentous fungi can also provide a vector for bacteria by transporting them to new locations where they may access new niches or substrates, as was observed for the degradation of polycyclic aromatic hydrocarbon pollutants (Kohlmeier *et al.*, 2005) This may have relevance in other contexts as well; for example, it has been postulated that the association of *Staphylococcus aureus* with Candida hyphae provides a mechanism for the bacterial invasion of otherwise inaccessible tissues, such as epithelial layers (Peters *et al.*, 2010). BFIs may also favor the colonization of surfaces that are otherwise

inaccessible to some microorganisms. *C. albicans* was shown to strongly enhance biofilm formation by *Staphylococcus aureus* in an in vitro polystyrene-serum system, with the bacteria associating with the fungal hyphae rather than the plastic substrate as part of a polymicrobial biofilm (Harriott and Noverr, 2010). Similar effects may be important for the colonization of medical devices by a range of microbes (Donlan and Costerton, 2002).

Role of BFIs in Host Health and Disease

The efforts of ants to control the parasitic fungi that attack their fungal gardens are paralleled by the attempts made by humans to control fungal diseases of plant crops. It has been recognized for a long time that many bacteria living in the root environment are able to promote plant health and growth (Lugtenberg and Kamilova, 2009) and that in some cases this is a consequence of their antagonistic impact on fungal pathogens in the soil (Weller *et al*, 2002). There is a large body of literature describing the use of rhizosphere bacterial isolates as potential "biocontrol" agents targeting a variety of soil borne fungal pathogens, indicating the potential of biocontrol bacteria to complement or even replace the application of chemical fungicides (Haas and Défago, 2005). Indeed, several commercial biocontrol agents targeting pre- and postharvest fungal diseases are available (Berg, 2009). However, despite meeting with a high degree of success in controlled environments, the widespread use of biocontrol bacterial strains is challenging, since each crop protection strategy is to some extent unique due to differences in cultivars, soil chemistries, and environmental conditions (Haas and Défago, 2005). Moreover, the usefulness of particular strains is not always predictable, mainly because of the variable abilities of the biocontrol bacteria to compete with resident rhizobacteria during root colonization, although they are often more efficient in disturbed natural ecosystems (Compant *et al*., 2005). In some instances, attempts have been made to use combinations of bacterial and fungal biocontrol agents to afford plants better protection from disease (Guetsky *et al*., 2001). Whether interactions between the biocontrol agents has affected the outcome of these tests has generally not been investigated, except in the case of *P. fluorescens* CHA0 and *Trichoderma atroviride*, which appear to have enhanced the expression of key biocontrol factors in each other's presence (Lutz *et al*., 2004). As well as the plant-beneficial bacterial-fungal relationships, one should not forget that some plant-detrimental BFIs also take place. Associated bacteria were shown to enhance the pathogenicity of the foliar fungal pathogen Stagonospora nodorum when infecting wheat, even though the bacteria themselves were nonpathogenic toward the host (Dewey *et al*., 1999). Synergistic interactions between Pectobacterium atrosepticum and Erwinia carotovora subsp. atroseptica and the foliar pathogen Septoria tritici on wheat have also been reported (Newton *et al*., 2004). In the rhizosphere, different functions can coexist, with Pseudomonas bacteria increasing or decreasing the plant pathogenesis of the soil borne fungus Gaeumannomyces (Sarniguet *et al*., 1992). The antimitotic toxin rhizoxin is an important component in the pathogenicity of the rice seedling blight pathogen Rhizopus microsporus; however, the synthesis of rhizoxin is performed not by the fungus but by Burkholderia_bacteria living within its hyphae (Partida-Martinez *et al*., 2005).

REFERENCES

Adams, A. S., Currie, C. R., Cardoza, Y., Klepzig, K. D. and Raffa, K. F. 2009. Effects of symbiotic bacteria and tree chemistry on the growth and reproduction of bark beetle fungal symbionts. *Can. J. Forest Res*, 39:1133– 1147.

Artursson, V. 2005. Bacterial-fungal interactions highlighted using microbiomics: potential application for plant growth enhancement. Ph.D. thesis. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Barbicri E., Ccccaroli, P., Sallarclli, R., Guidi, C., Polcnza, L., Basaglia, M., Fonlana, F., Baldan, E., Casclla, S. and Ryahi, O. 2010. New evidence for nitrogen fixation within the Italian white truffle *Tuber magnatum*. Fungal Biol, 114:936–942.

Bates, S. T., Cropsey, G. W., Caporaso, J. G., Knight, R. and Fierer, N. 2011. Bacterial communities associated with the lichen symbiosis. Appl. Environ. Microbiol, 77:1309–1314.

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

Bertaux, J., Schmid, M., Hutzler, P., Hartmann, A., Garbaye, J. and Frey-Klet, P. 2005. Occurrence and distribution of endobacteria in the plant-associated mycelium of the ectomycorrhizal fungus *Laccaria bicolour* S238N. *Environ. Microbiol*, 7:1786–1795.

Bianciotto, V., Genre1, A., Jargeat, P., Lumini, E., Bécard, G.and Bonfante, P. 2004. Vertical transmission of endobacteria in the arbuscular mycorrhizal fungus *Gigaspora margarita* through generation of vegetative spores. *Appl. Environ. Microbiol*, 70:3600–3608.

Bianciotto, V., Andreotti, S., Balestrini, R., Bonfante, P. and Perotto, S. 2001. Extracellular polysaccharides are involved in the attachment of *Azospirillum brasilense* and *Rhizobium leguminosarum* to arbuscular mycorrhizal structures. *Eur. J. Histochem*, 45:39–49.

Bianciotto, V., Bandi, C., Minerdi, D., Sironi, M., Tichy, H. V. and Bonfante, P. 1996. An obligately endosymbiotic mycorrhizal fungus itself harbors obligately intracellular bacteria. *Appl. Environ. Microbiol*, 62: 3005–10.

Bianciotto, V., Lumini, E., Bonfante, P. and Vandamme, P. 2002. 'Candidatus Glomeribacter gigasporarum' gen. nov., sp. nov., an endosymbiont of arbuscular mycorrhizal fungi. *Int. J. Syst. Evol. Microbiol*, 53:121–24.

Bilger, W., Bu¨del, B., Mollenhauer, R. and Mollenhauer, D. 1994. Photosynthetic activity of two developmental stages of a *Nostoc* strain (Cyanobacteria) isolated from *Geosiphon pyriforme* (Mycota). *J. Phycol*, 30:225– 230.

Bonfante, P. 2003.Plants, mycorrhizal fungi and endobacteria: a dialog among cells and genomes. Biol. Bull, 204: 215–20.

Brand, A., Barnes, J. D., Mackenzie, K. S., Odds, F. C. and Gow, N. A. 2008. Cell wall glycans and soluble factors determine the interactions between the hyphae of *Candida albicans* and *Pseudomonas aeruginosa*. FEMS Microbiol. Lett, 287:48–55

Brule, C., Frey-Klett, P., Pierrat, J-C., Courrier, S., Gérard, F,, Lemoin, M-C., Roussellet, J-L., Sommer, J. and Garbaye,

J. 2001. Survival in the soil of the ectomycorrhizal fungus *Laccaria bicolor* and the effects of a mycorrhiza helper *Pseudomonas fluorescens*. *Soil Biol. Biochem*, 33:1683–1694.

Calvo, A. M., Wilson, R. A., Bok, J. W. and Keller, N. P. 2002. Relationship between secondary metabolism and fungal development. *Microbiol. Mol. Biol. Rev*, 66:447–459.

Chandelier, A., Abras, S., Laurent, F., Debruxelles, N. and Cavelier, M. 2006. Effect of temperature and bacteria on sporulation of *Phytophthora alni* in river water. *Commun. Agric. Appl. Biol. Sci*, 71:873–880.

Compant, S., Duffy, B., Nowak, J., Clement, C. and Barka, E. A. 2005. Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Appl. Environ. Microbiol*, 71:4951–4959.

Deveau, A., Brulé, C., Palin, B., Champmartin, D., Rubini, P., Garbaye, J., Sarniguet, A. and Frey-Klett, P. 2010. Role of fungal trehalose and bacterial thiamine inthe improved survival and growth of the ectomycorrhizal fungus *Laccaria bicolor* S238N and the helper bacterium *Pseudomonas fluorescens* BBc6R8. *Environ. Microbiol. Rep*, 2:560–568.

Dewey, F. M., Wong, Y. L., Seery, R., Hollins, T. W. and Gurr, S. J. 1999. Bacteria associated with *Stagonospora (Septoria) nodorum* increase pathogenicity of the fungus. New Phytol, 144:489–497.

Donlan, R. M. and Costerton, J. W. 2002. Biofilms: survival mechanisms of clinically relevant microorganisms. Clin. Microbiol. Rev, 15:167–193.

Elad, Y. and Baker, R. 1985. The role of competition for iron and carbon fungi in the cucumber rhizosphere. Appl. Environ. Microbiol, 67:1851– 1864.

Fajardo, A. and Martínez, J. L. 2008. Antibiotics as signals that trigger specific bacterial responses. *Curr. Opin. Microbiol*, 11:161–167.

Fleming, A. 1929. On the antibacterial action of cultures of a *Penicillium*, with special reference to their use in the isolation of *B. influenzae*. *Br. J. Exp. Pathol*, 10:226–236.

Gaddy, J. A., Tomaras, A. P. and Actis, L. A. 2009. The *Acinetobacter baumannii* 19606 OmpA protein plays a role in biofilm formation on abiotic surfaces and in the interaction of this pathogen with eukaryotic cells. Infect. Immun, 77:3150–3160.

Guetsky, R., Shtienberg, D., Elad, Y. and Dinoor, A. 2001. Combining biocontrol agents to reduce the variability of biological control. Phytopathology, 91:621–627.

Haas, D. and Defago, G. 2005. Biological control of soil-borne pathogens by fluorescent *pseudomonads*. Nat. Rev. Microbiol, 3:307–319.

Harriott, M. M. and Noverr, M. C. 2010. Ability of Candida albicans mutants to induce Staphylococcus aureus vancomycin resistance during polymicrobial biofilm formation. Antimicrob. Agents Chemother, 54:3746–3755.

Hoffman, M. T., and Arnold, A. E. 2010. Diverse bacteria inhabit living hyphae of phylogenetically diverse fungal endophytes. *Appl. Environ. Microbiol*, 76:4063–4075.

Hogan, D., Vik, A. and Kolter, R. 2004. A *Pseudomonas aeruginosa* quorumsensing molecule influences *Candida albicans* morphology. Mol. Microbiol, 54:1212–1223

Kluge, M. 2002. A fungus eats a cyanobacterium: the story of the *Geosiphon pyriformis* endocyanosis. Biol. Environ, 102:11–14.

Kobayashi, D. Y., Reedy, R. M., Palumbo, J. D., Zhou, J-M. and Yuen, G. Y. 2009. A clp gene homologue belonging to the Crp gene family globally regulates lytic enzyme production, antimicrobial activity, and biological control activity expressed by *Lysobacter enzymogenes* strain C3. *Appl. Environ. Microbiol*, 71:261–69.

Kohlmeier, S., Smits, T. H. M., Ford, C. R., Keel, M., Harms, H. and Wick, L. Y. 2005. Taking the fungal highway: mobilization of pollutant-degrading bacteria by fungi. *Environ. Sci. Technol*, 39:4640–4646.

Linares, J. F., Gustafsson, I., Baquero, F. and Martinez, J. L. 2006. Antibiotics as intermicrobial signaling agents instead of weapons. Proc. *Natl. Acad. Sci*, U. S. A 103:19484–19489.

Lugtenberg, B. and Kamilova, F. 2009. Plant-growth-promoting rhizobacteria. Annu. Rev. Microbiol, 63:541–556.

Lumini, E., Ghignone, S., Bianciotto, V. and Bonfante P. 2006. Endobacteria or bacterial endosymbionts? To be or not to be. New Phytol, 170:205–208.

Lutz, M. P., Wenger, S., Maurhofer, M., Defago, G. and Duffy, B. 2004. Signaling between bacterial and fungal biocontrol agents in a strain mixture. FEMS Microbiol. Ecol, 48:447–455

Moller, J., Miller, M. and Kjoller, A. 1999. Fungal-bacterial interaction on beech leaves: influence on decomposition and dissolved organic carbon quality. Soil Biol. Biochem, 31:367–374.

Newton, A. C., Toth, I. K., Neave, P. and Hyman, L. J. 2004. Bacterial inoculum from a previous crop affects fungal disease development on subsequent non host crops. New Phytol, 163:133–138.

Noble, R., *et al*. 2003. Primordia initiation of mushroom (*Agaricus bisporus*) strains on axenic casing materials. Mycologia, 95:620–629

O'May, G. A., Reynolds, N., Smith, A. R., Kennedy, A. and Macfarlane, G. T. 2005. Effect of pH and antibiotics on microbial overgrowth in the stomachs and duodena of patients undergoing percutaneous endoscopic gastrostomy feeding. *J. Clin. Microbiol*, 43:3059–3065.

Odum, E. P. 1953. Fundamentals of Ecology. W. B. Saunders, Philadelphia / London.

Palla, F., Marineo, S., Lombardo, G. and Anello, L. 2006. Characterization of bacterial community in indoor environment, p. 361–365. In R. Fort, M. Alvarez de Buergo, M. Gomez-Heras, and C. Vazquez-Calvo (ed.), Heritage, weathering, and conservation: proceedings of the international conference, HWC-2006. Taylor & Francis, London, United Kingdom.

Partida-Martinez, L. P., Flores de Looss, C., Ishida, K., Ishida, M. and Roth, M., 2007, Rhizonin, the first mycotoxin isolated from the Zygomycota, is not a fungal metabolite but is produced by bacterial endosymbionts. *Appl. Environ. Microbiol*, 73:793–97.

Peters, B. M., Jabra-Rizk, M. A., Scheper, M. A., Leid, J. G., Costerton, J.W. and Shirtliff, M. E. 2010. Microbial interactions and differential protein expression in *Staphylococcus aureus-Candida albicans* dual-species biofilms. *FEMS Immunol. Med. Microbiol*, 59:493–503.

Pinto-Tomas, A. A., Anderson, M. A., Suen, G., Stevenson, D. M., Chu, F. S. T., Cleland, W. W., Weimer, P. J. and Currie, C. R. 2009. Symbiotic nitrogen fixation in the fungus gardens of leaf-cutter ants. Science, 326:1120–1123.

Riedlinger, J., Schrey, S. D., Tarkka, M. T., Hampp, R., Kapur, M. and Fiedler, H. P. 2006. Auxofuran, a novel metabolite that stimulates the growth of fly agaric, is produced by the mycorrhiza helper bacterium *Streptomyces* strain AcH 505. *Appl. Environ. Microbiol*, 72:3550–3557.

Sarniguet, A., Lucas, P., Lucas, M. and Samson, R. 1992. Soil conduciveness to take-all of wheat: influence of the nitrogen fertilizers on the structure of populations of fluorescent pseudomonads. Plant Soil, 145:29–36.

Schoonbeek, H. J., Jacquat-Bovet, A. C., Mascher, F. and Metraux, J. P. 2007. Oxalate-degrading bacteria can protect *Arabidopsis thaliana* and crop plants against *Botrytis cinerea*. *Mol. Plant Microbe Interact*, 20:1535–1544.

Schouten, A., Maksimova, O., Cuesta-Arenas, Y., van den Berg, G. and Raaijmakers, J. M. 2008. Involvement of the ABC transporter BcAtrB and the laccase BcLCC2 in defence of *Botrytis cinerea* against the broad-spectrum antibiotic 2,4-diacetylphloroglucinol. *Environ. Microbiol*, 10:145–157

Tarkka, M. T., Sarniguet, A. and Frey-Klett, P. 2009. Inter-kingdom encounters: recent advances in molecular bacterium-fungus interactions. Curr. Genet, 55:233–243.

Uroz, S., and Heinonsalo, J. 2008. Degradation of N-acyl homoserine lactone quorum sensing signal molecules by forest root-associated fungi. FEMS Microbiol. Ecol, 65:271–278.

Wade, W. N. and Beuchat, L. R. 2003. Metabiosis of proteolytic moulds and Salmonella in raw, ripe tomatoes. *J. Appl. Microbiol*, 95:437–450.

Wargo, M. J. and Hogan, D. A. 2006. Fungal-bacterial interactions: a mixed bag of mingling microbes. *Curr. Opin. Microbiol*, 9: 359–64.

Weller, D. M., Raaijmakers, J. M., Gardener, B. B. and Thomashow, L. S. 2002. Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annu. Rev. Phytopathol*, 40:309–348.

****