REVIEW

Phylloplane microbes impact host physiology: a review

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Abstract

The phyllosphere refers to the entire aerial habitat of plants while phylloplane describes the entire leaf surface. The phylloplane provides a niche for diversified microbial communities and as such it is an important ecosystem both ecologically and economically. For many years, phylloplane dwellers have been studied as bio protectants and enhancers of growth in host plants. Plants and phylloplane-microbial-interactions result in increased fitness and productivity of agricultural crops. In this study, an attempt was made to compile previous studies in order to better understand the role of phylloplane microbiota in influencing the physiology of flora. We also proposed possible further research to explore molecular aspects of signaling mechanisms established by the phylloplane microbial community with their hosts which impact the latter's physiology.

Keywords: bioprotectants, epiphytes, microbiota, phylloplane, phyllosphere

Introduction

Microorganisms inhabit almost all plant tissues (Turner *et al.* 2013). The phyllosphere (the entire aerial habitat) and phylloplane (the leaf surface) thus harbor a multitudinous microbial community. These phylloplane microbes when associated with plant surfaces are called epiphytes and when they reside inside tissues they are called endophytes (Arnold *et al.* 2000). The epiphytes are present in both adaxial and abaxial regions (Andrews and Harris 2000). Extensive studies on rhizospheric microbial communities have paved the way to understand their direct involvement in crop productivity, protection against pathogens and stimulating plant growth by inducing the release of phytohormones in the host cells. Caulier *et al.* (2018) screened *Bacillus* and *Pseudomonas* spp. strains against potato pathogens and concluded that rhizosphere microflora are effective biomanagement tools. Rhizosphere microorganisms, like *Trichoderma* spp., *Bacillus*, *Pseudomonas* and *Streptomyces*, have been exploited for management of fungal diseases (Toyota and Shirai 2018). However, the phylloplane, which is comprised of photosynthetic leaves, harbors hyperdiverse

microbiota and has always been a fascinating field for researchers. The diverse microbial communities which inhabit the leaves include bacteria, fungi, algae, yeasts and nematodes (Whipps *et al.* 2008). Among all plant tissues, the leaf surface provides the optimum environment for microflora since the leaf exudates supply them with nutrition, moisture, pH and temperature for survival (Shukla and Sharma 2016). Plants and phylloplane-microbe-interactions contribute to the growth, development and protection of plants (Lindow and Brandl 2003). According to Rastogi *et al.* (2012) and Bulgarelli *et al.* (2013) about 6.4×10^8 km^2 terresetrial leaf surface area is inhabited by microbes. Most phytopathogens enter plants via the phylloplane. Sometimes phytopathogens overcome plant defense by colonization as well as competing with resident microorganisms (Bringel and Couée 2015). Among the entire microbial population, the phylloplane seems to be most suitable for bacteria since its numbers range from 10^5 to 10^7 cells per gram of leaf (Yadav *et al.* 2010). Fungal spores are also accomodated by the leaves which are exposed to a continuous air current

which carry the spores (Shukla and Sharma 2016). Leaves trap fungal spores through waxy surfaces and trichomes (Saleem and Paul 2016) and when a suitable microhabitat is found, they form colonies and maintain their existence. Although fewer in population than bacteria, phylloplane fungi are known to play significant ecophysiological roles such as interaction with pathogenic fungi, carbon/nitrogen dynamics or preliminary steps of leaf litter degradation (Voříšková and Baldrian 2013). Phyllosphere dominating microbes include *Methylobacterium*, *Sphingomonas*, *Pseudomonas* among bacterial populations (Bodenhausen *et al.* 2013; Kembel *et al.* 2014) while fungal communities include members of Ascomycota and Basidiomycota (Jumpponen and Jones 2010). Phylloplane microbes have been explored and found to play an important role in antimicrobial (i.e antibacterial and antifungal) activities against phytopathogens (Mazinani *et al.* 2017). The antagonistic behavior of microbes is due to the competitive existence in their environment by diminishing the growth of other pathogens (Chaudhary *et al.* 2017). Microbial communities produce antimicrobial compounds against their rivals (Braun *et al.* 2010). Antimicrobial compounds secreted by phylloplane microfungi on aerial surfaces can be directly detrimental to pathogens or via induction of systemic acquired resistance (SAR) in the plant cells (Lindow and Brandl 2003). Phylloplane microbiota promotes plant growth through the production of phytohormones e.g., indole acetic acid (IAA), cytokinins, etc. *Sphingomonas* spp. have been found to produce plant growth stimulating factors i.e., IAA which suggest that plant hormones produced by phyllospheric bacteria enhance plant growth (Enya *et al.* 2007). Microorganisms are also known to play an important role in global processes like nitrogen fixation, nitrification and phosphate solubilization (Furnkranz *et al.* 2008; Mwajita *et al.* 2013). Global links between plant nitrogen balance and leaf epiphytic bacterial species richness has also been observed (Manching *et al.* 2014). Phylloplane microbes have been studied to understand their role in photosynthesis, one of the most important physiological phenomenon in nature. Studies reveal that phylloplane microfungal metabolites have enhanced the activity of Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) thus playing an important role in the photosynthetic process (Mitra *et al.* 2014). However, to better understand the molecular mechanisms as well as how and why these phylloplane microbes actually affect the physiology more exploration is needed. Studies on the behavior of the leaf protein profile of the host can be a tool to understand phylloplane microbe interactions. The expression or suppression of certain proteins would help us to know more about the impact of phylloplane microbes on the host.

Phylloplane microbes as bioprotectants

Non-pathogenic beneficial microbes directly interact with plant pathogens by secreting chemical metabolites (Dey *et al.* 2014). Siderophores produced by iron competing bacteria, antibiotics such as DAPG and pyocyanin, biosurfactants such as 2R, 3R-butanediol produced by *B. subtilis* GBO_3 (130) and a C_{13} volatile emitted by *Paenibacillus polymyxa* are chemical metabolites which can protect plants (Pieterse *et al.* 2014). Phyllospheric microbes, mainly bacteria and fungi, act as beneficial mutualists that improve plant growth and also act as antagonistic pathogens (Bringel and Couée 2015; Stone *et al.* 2018). According to Harish *et al.* (2007), phylloplane fungi such as *Cladasporium* spp., *Penicillium* spp., and *Aspergillus flavus* could inhibit mycelial growth and spore germination of *Helminthosporium oryzae* thus preventing rice brown spot. According to Alam *et al.* (2010), *Penicillium* spp. isolated from tomato and cabbage were effective against *Fusarium oxysporum*. Under controlled laboratory conditions, *Sphingomonas* strains suppressed disease symptoms and reduced the growth of *Pseudomonas syringae* pv. *syringae* DC3000 on *Arabidopsis thaliana* leaves (Innerebner *et al.* 2011). The metabolites of *Trichoderma viride* and *Aspergillus flavus* were found to be effective in inhibiting the pathogenicity of *Alternaria brassicae* against rabi crops (Yadav *et al.* 2011). Kuberan *et al.* (2012) demonstrated that *T. viride* could be efficiently used as a biocontrol agent against *Glomerella cingulate* in tea. Chowdappa *et al.* (2013) reported that *T. harzianum* OTPB3 and *Bacillus subtilis* OTPB1 were antagonistic towards *Alternaria solani* and *Phytophthora infestans* and could also result in induction of systemic resistance in tomato seedlings against early and late blight. The phylloplane bacterium *Ochrobactrum anthropi* BMO-111 was found to be effective against blister blight disease of tea caused by *Exobasidium vexans* (Sowndhararajan *et al.* 2013). *Bacillus* and *Stenotrophomonas* genera in their phyllosphere microbial communities showed antagonistic potential towards *Botrytis cinerea* (Ortega *et al.* 2016). *Trichoderma harzianum* ISO-2 and *Penicillium sublateritium* showed efficacy against *Alternaria alternata* causing leaf spot in *Rauwolfia serpentina* (Thakur 2016). *Serratia plymuthica* isolates (UBCF_01 and UBCF_13) were found to exhibit suppression activity against *Colletotrichum gloeosporioides* (Aisyah *et al.* 2017). *Streptomyces viridosporus*, *T. harzianum* and *T. viride* were seen to control *Plasmopara viticola* causing downy mildew of grapevine (El-Sharkawy *et al.* 2018). Plant growth promoting fungi (PGPF) have gained attention by virtue of their role in maintaining plant quality and quantity. *Alternaria* spp., *Trichoderma* spp., *Ganoderma* spp., and *Saccharomyces* spp. have been extensively studied as PGPFs (Abdelrahman *et al.*

2016; Jogaiah *et al.* 2016; Zhou *et al.* 2018; Baiyee *et al.* 2019). According to Baiyee *et al.* (2019), *T. asperellum* could induce peroxidase and polyphenol oxidase and also cell wall degrading enzymes, namely chitinase and β-1,3-glucanase in lettuce plants as a defensive mechanism against leaf spot disease.

The role of phylloplane microbes in systemic aquired resistance (SAR) and induced systemic resistance (ISR)

Phylloplane microbes can be directly detrimental to host pathogens through production of antimicrobial compounds, or they may be involved in plant protection through an indirect mechanism, induced systemic resistance (ISR) or systemic acquired resistance (SAR) (Fig. 1). SAR is activated throughout a plant by exposure to elicitors from virulent, avirulent or nonpathogenic microbes or artificial stimuli while ISR is the resistance mechanism in plants which become activated on infection due to an invading pathogen (Kamle *et al.* 2020). He *et al.* (2002) reported that nonpathogenic *F. oxysporum* could induce systemic resistance and defense responses against pathogenic *F. oxysporum* f. sp. *asparagi* in *Asparagus officinalis*. Dong *et al.* (2003) demonstrated that water extracts of dry mycelium of *P. chrysogenum* (PEN) when applied to the roots of *Gossypium hirsutum* cultivars (H552 and Vered) and *G. barbadense* cultivars (PF15 and P906) increased

peroxidase (POX) activity which resulted in lignification and hence was associated with defense. The fungal elicitors from *F. oxysporum* (non-virulent strains) when applied to banana against Panama disease elicited SAR (Patel *et al.* 2004). Halfeld-Vieira *et al.* (2006) concluded that the phylloplane resident bacteria *Bacillus cereus* isolated from healthy tomato plants was responsible for ISR against *P. syringae* pv. *tomato*. Mathivanan *et al.* (2008) reported the enhancement of POX activity in plants treated with fungal metabolites. Studies by Nicot (2011) revealed that *Trichoderma* produced a toxic compound which had antimicrobial activity against pathogens as well as secreting compounds that stimulated the plant to produce its own defense metabolites. According to Gherbawy *et al.* (2012), *Fusarium* spp. were effective in increasing POX activity in shoots of wheat infected with pathogenic *Fusarium* spp. Buxdorf *et al.* (2013) reported that local inoculation of *Pseudozyma aphidis* elicited induced resistance in *Arabidopsis* and reduced growth of *Botrytis cinerea* on local and systemic leaves. There have been reports that pre-treatment of tomato and cucumber plants with epiphytic fungus *Pseudozyma aphidis* spores suppressed bacterial canker caused by *Clavibacter michiganensis* and powdery mildew caused by *Podosphaera xanthii* and thus triggered an induced resistance response (Barda *et al.* 2015; Gafni *et al.* 2015). *Pseudomonas fluorescens* talc (Pf1) was used as a biocontrol against *Magnaporthe oryzae*,
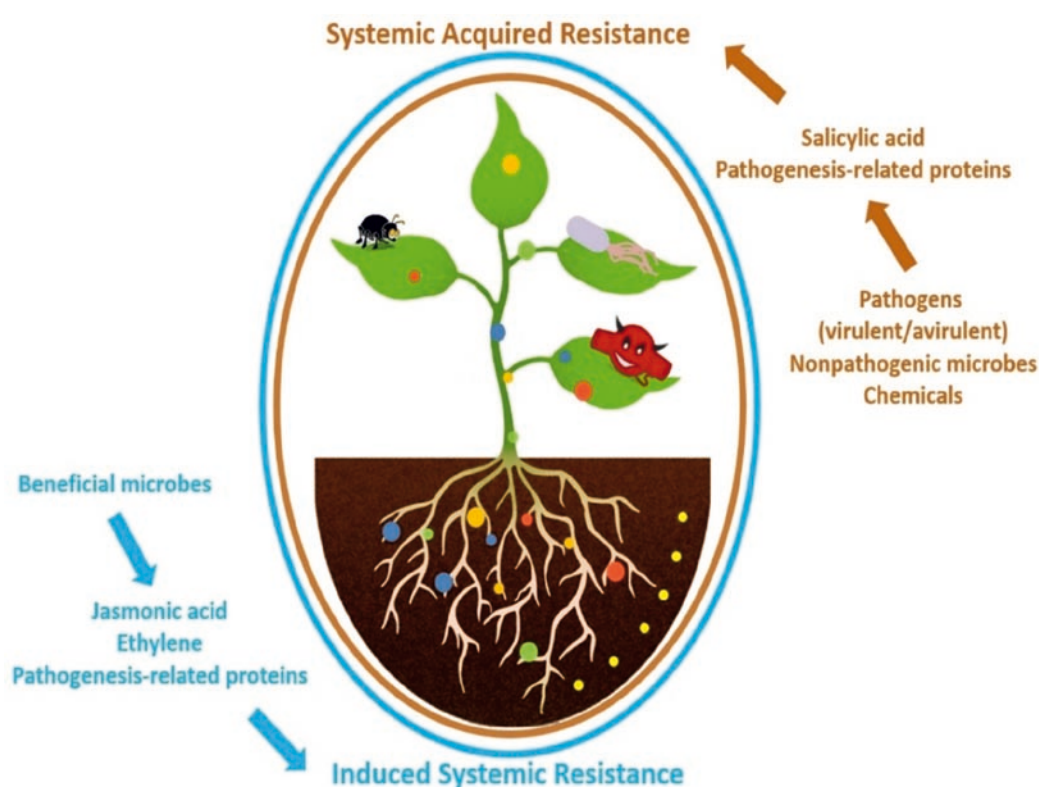

Fig. 1. Microbial and bioactive soil amendments for improving strawberry crop growth, health, and fruit yields: a 2017–2018 study (Dara 2019)

an ascomycete fungus that caused rice blast. It significantly triggered the activity of defense related enzymes viz: peroxidase (PO), polyphenol oxidase (PPO) and phenylalanine ammonia lyase (PAL). This result was observed due to induced systemic resistance (ISR) (Suguna *et al*. 2020). Moreover, induced resistance was also observed against plant viruses. Su *et al*. 2017 investigated the ability of *Rhodopseudomonas palustris* GJ-22 to induce resistance against tobacco mosaic virus (TMV) while promoting plant growth.

Phylloplane microbes enhance the productivity of crops

Phyllospheric microorganisms play crucial roles in plant growth and thus provide ecosystem services like carbon (C) sequestration, nitrogen (N) fixation and bioremediation, thereby enhancing crop yield and improving soil health (Bulgarelli *et al*. 2013). The presence of nitrogen fixing bacteria has been reported in phyllosphere community composition surveys (Delmotte *et al*. 2009; Holland 2011). Under temperate conditions, nitrogen fixation occurs in the interior tissues while in a tropical environment, nitrogen fixation occurs in the phyllosphere because more moisture on the leaf surface allows nirogen fixing bacteria to be active (Furnkranz *et al*. 2008). Nitrogen fixing microorganisms when sprayed onto leaves can promote plant growth and increase the nitrogen content of plants (Giri and Pati 2004). Marques *et al*. (2010) reported that plant growth promoting (PGP) bacteria isolated from *Zea mays* produced IAA, hydrogen cyanide (HCN) and ammonia *in vitro* as well as in greenhouse experiments. Mwajita *et al*. (2013) isolated phyllosphere bacteria from rice fields in Kenya and reported that over 50% of the isolates were able to solubilize phosphates. According to Esitken *et al*. (2010) inoculation of *Bacillus* M3 and spraying of *Pseudomonas* BA-8 or *Bacillus* OSU-142 potentially increased the yield, growth and P, Fe, Cu and Zn content of strawberry plants. M3+BA-8, BA-8-+OSU-142, M3, M3+OSU-142 and BA-8 applications increased cumulative yield by 33.2%, 18.4%, 18.2%, 15.3% and 10.5%, respectively. There was a significant increase in the number of fruits per plant with the application of M3+BA-8 (91.73%) and M3 (81.58%) as compared to the control (68.66%).

Phyllosphere microorganisms also play a protective role by oxidizing ammonia to nitrate through nitrification (Guerrieri *et al*. 2015). Studies by Bowatte *et al*. (2015) and Watanabe *et al*. (2016) showed that chemoautotrophic nitrifiers, like-archea have been identified in the phyllosphere of a number of plant species.

Several phylloplane inhabiting microbes produce phytohormones such as auxin, gibberellic acids, and cytokines and could fix nitrogen and mobilize nutrients (Dourado *et al*. 2015). Indole acetic acid is also produced by phyllospheric microorganisms which stimulates root growth and eventually enhances root contact with soil and increases nutrient uptake. Due to this ability, such phylloplane microbial inoculants as: *Bacillus*, *Microbacterium*, *Acinetobacter*, *Proteus*, *Psychrobacter*, *Pseudomonas*, etc., are now recommended as substitutes to chemical fertilisers (Batool *et al*. 2016; Mohanty *et al*. 2016). In another study, 12 yeast strains were isolated from *Drosera indica* L. that were able to produce IAA which modify auxin inducible gene expression in *Arabidopsis* thus show that phyllospheric yeasts which can promote plant growth, can be considered as biofertilizer for sustainable agriculture (Sun *et al*. 2014). Studies performed by Batool *et al*. (2016) indicated that phylloplane bacteria isolated from wheat varieties had better PGP abilities in high yielding varieties. Seher phylloplane isolates produced the highest amount of auxin (52.95 $\mu g \cdot ml^{-1}$).

Phylloplane microbes influence plant cell organelles (chloroplasts)

Studies have revealed that biotic and abiotic stress can damage plant organelles. Bowes (1991) reported that pathogen inoculation in plants reduced the concentration of Rubisco, a key photosynthetic enzyme. The catalytic activity of Rubisco got depleted thus reducing its K_m that is the enzyme's affinity for the substrate, much below the threshold value. Moreover, biotic stress also reduced V_{max} (rate attained when the enzyme sites are saturated) values in tomato plants emphasizing on the fact that stress depletes Rubisco activity. Earlier research reported that the photosynthetic yield in plants has been shown to be significantly reduced by pathogen infection (Berger *et al*. 2007; Wang *et al*. 2014). Phylloplane microbes have also been studied and exploited to induce defence responses in plants against phytopathogens. Some strains of *Trichoderma* spp. and *Sebacinales* spp. had been identified as biocontrol fungi also showing the ability to improve photosynthetic efficiency of plants (Shoresh *et al*. 2010). Carbon dioxide (CO_2) assimilation in plants increased due to enhanced Rubisco activity, resulting into higher productivity (Shoresh *et al*. 2010). Mitra *et al*. (2014) reported that the metabolites of phylloplane fungi like *A. niger* and *F. oxysporum* not only masked the effect of pathogens but also upregulated Rubisco activity in tomato plants.

Carbonic anhydrase (CA), another important enzyme found in chloroplast, also plays a crucial role in photosynthesis and respiration in plants. Sunderhaus *et al*. (2006) reported that chloroplast CA is important in efficiently delivering CO_2 to Rubisco. Studies by Di Mario *et al*. (2017) disclosed that CA converted

the accumulated bicarbonates into CO_2 which is converted into carbohydrates by plants and its fixation was done by Rubisco. According to Hudson *et al.* (1992), changes in CA activity also affected the concentration of Rubisco which implied that both enzymes are functionally interdependent. The activity of CA in pea was enhanced by phylloplane fungal metablites (Majeau and Coleman 1994), which otherwise get depleted due to pathogen attack, thus resulting in effective photosynthesis (Mitra *et al.* 2019).

Phylloplane microbes influence plant cell organelles (mitochondria)

It has also been observed that mitochondrial physiology is impacted by phylloplane microbes. Succinate dehydrogenase (SDH) located in the inner membrane of mitochondria influences photosynthesis, induces fungal defense responses in plants and controls stomatal functions and root elongation (Huang and Millar 2013). Plants inoculated with *Pseudomonas syringae* pv. *tomato* exhibited reduced SDH activity (Mitra *et al.* 2013). Ahmad and Prasad (2011) concluded that succinate oxidation to fumarate by CO_2 leads to inhibition of SDH leading to succinate accumulation which is toxic to plant tissues. Studies revealed that anomalies in SDH lead to reduction of mitochondrial H_2O_2 production and to an increase in host susceptibility against pathogens (O'Brien *et al.* 2012). Toivonen and Hodges (2011) reported that high CO_2 levels inhibit SDH thus affecting the tricarboxylic acid (TCA) cycle and aerobic respiration causing several physiological disorders in hosts. Thus, any physiological or chemical alterations in the mitochondrial environment resulted in its destruction and hence respiratory levels of the plant are affected badly resulting in plant wilt and death. However, SDH activity in *Cerasus sachalinensis* was increased when the plants were treated with soil microbes (Qin *et al.* 2014). A combination of phylloplane fungal metabolites was also seen to significantly elevate the SDH activity which might indicate that net SDH activity is a function of combined activities of all phylloplane microbes (Paul and Mitra 2013).

Molecular mechanism of plant microbe interaction

Phyllospheric microorganisms, being dwellers of sunlight exposed habitats can grow in a nutrient limited environment because of the availability of carbon and energy through photochemical conversion of light resources by the host (Chaudhary *et al.* 2017). Through metagenomic data analysis the presence of rhodopsin genes in phyllospheric communities has been observed. This can be activated by radiations and can cover wavelengths distinct from the absorption spectrum of chlorophyll and carotenoides thus enhancing the process of photosynthesis and eventually producing plant carbon resources which are utilized by epiphytic microorganisms (Atamna-Ismaeel *et al.* 2012; Stiefel *et al.* 2013). According to Singh *et al.* (2016), in the presence of beneficial microbes, plants which are stressed due to pathogen attack reprogramed their metabolic pathways involved in defense. Salicylic acid and jasmonic acid are the plant hormones which play key roles in the signal transduction process induced by beneficial microbes and the process was termed as "priming" (Delaney 1997; Conrath *et al.* 2002). Priming was identified as a mode of action in *Pseudomonas fluorescence* strain WCS417r where the strain when applied to *Arabidopsis thaliana* stimulates a host response effective against *Pseudomonas syringae* (van Wees *et al.* 2000).

Conclusions and future prospects

Phyllosphere microbiology has been extensively studied for decades against various parameters to understand the ecology of the microbial community and their functionality in association with plant hosts. Most studies on phyllosphere microbial communities are limited to diversity and characterization of epiphytic microbes on different phylloplane hosts. These phyllosphere microbes have been shown to be instrumental in manipulating the host physiology both positively and negatively, in order to survive on their surfaces. Usually, they are harmful to hosts, but several instances have been observed where the phylloplane microbes have a mutualistic beneficial relationship, allowing the microbes to withstand environmental pressure, receive nutrition and conducive conditions for sustanance from the host plants and in turn stimulate a wide range of physiological processes in the hosts, leading to their growth, development and protection. Undoubtedly, the phylloplane microbes have much more to contribute to plant protection, physiology and to agriculture. Furthermore, such findings will substantiate the idea that commensal microbiota on phylloplane can play a key role in pathogen exclusion contributing to plant health and productivity and present practical applications to develop novel strategies for prediction and prevention of diseases. However, the molecular mechanisms underlying the interaction of phylloplane microbiome with the host plants need more exploration. Interactive studies like quorum sensing may help us to learn about loose associations intimate to symbiosis between plants and microbes. Molecular studies can help scientists to better understand the extent to which phyllosphere microbiota can interact with microbe-associated molecular

patterns thus triggering plants' innate immunity. These studies can help to broaden our knowledge on health and protection of plants. It is now known that these phylloplane microorganisms are able to enhance the activity of some important plant enzymes associated with plant physiology, but it needs to be established through modern molecular technologies. The underlying principles of signaling cascade and signal transduction established during compatible host-microbe interaction must be investigated in order to better understand their key roles in plant performance, growth, defense and better plant functioning. Studies focusing on isolation and identification of protein profiles responsible for expression or suppression of host genes due to the phylloplane microbes will help in the understanding of the actual causes of the impact of the host-microbe interaction. The amalgamation of metagenomics, proteomics, laboratory and land experiments may definitely assert our study and give new insights into the pivotal role of phylloplane microbial communities in global processes, plant health and physiology, leading to their contribution to the changing world.

Acknowledgements

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