
Prospect of Phyllosphere Microbiota: A Case Study on Bioenergy Crop *Jatropha curcas*

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Abstract

Phyllosphere is the most abundant environment that supports microbial life. This ecosystem is a stress environment characterized by fluctuation in moisture, nutrients, radiation and plant's own immune system. However, plants support microbial community on the phyllosphere as a strategy for its survival and growth. This chapter addresses general characterization of phyllospheric environment, microbial association process, microbial population structure, quorum sensing and cross talk between plant and microbes. This chapter provides information on the microbial diversity of the phyllosphere of bioenergy crop *Jatropha curcas*. Major bacterial groups prevalent on the *J. curcas* phyllosphere and plant growth-promoting activities are addressed.

20.1 Introduction

Phyllosphere is one of the large habitats for microbial population accounting for $\sim 6.4 \times 10^8$ km² on the earth. Leaf surface supports extensive bacterial populations which can be as high as 10^7 cm⁻². It is estimated that phyllosphere bacterial population could be of 10^{26} cells in the tropical plants (Morris et al. 2002). The phyllosphere is a stress environment because it is controlled by external factors like temperature, moisture and solar radiation. It is also a low-nutrient environment. The phyllosphere provides environmental niche for different microorganisms. Bacteria are the most predominant groups of the phyllosphere. Plant modifies phyllospheric bacterial community by changing leaf exudates and moisture like regulating leaf moisture

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through stomata opening and closing. Some microorganisms invade into leaf tissue as a strategy to survive under water stress condition while others manage to survive under low moisture condition (Hardoim et al. 2008). The phyllospheric microorganisms play crucial role in plant's growth. These bacteria fix N and C protect plant from pathogens and produce phytohormones (Bulgarelli et al. 2013). Thus, the phyllospheric organisms provide ecosystem services like C sequestration, N fixation, and bioremediation, enhance crop yield and improve soil health (Bulgarelli et al. 2013). These microbial groups hold key to plant's solvability under extreme condition and sustainability in future climate change.

Jatropha curcas is also known as the biofuel/biodiesel crop. The *J. curcas* belongs to Euphorbiaceae family and is characterized as a drought-resistant perennial plant. It is propagated in tropical and subtropical countries for augmenting renewable energy. In addition, it has several beneficial properties that are significant for agriculture, ecology and environment. Plantation of *J. curcas* is generally recommended to manage degraded wasteland. *J. curcas*-derived biodiesel is a biodegradable and non-toxic fuel compared to petroleum-based diesel. *J. curcas* grows well in low to high rainfall areas. It is cultivated as a commercial crop or as a hedge plant to protect agricultural fields from grazing animals. It can improve socio-economic status of poor farmers in Third World countries as a resource for biodiesel. It is interesting that this plant doesn't need much input like other plants. It can grow under various stress condition like low nutrient and water input. It is hypothesized that microbiome of this plant may hold the key for its sustainability and growth under limited environmental conditions.

Recently many studies elucidate the diversity of microorganisms prevalent in the rhizosphere of *J. curcas*. It harbours significant numbers of arbuscular mycorrhizae like *Acaulospora* sp., *Gigaspora* sp., *Glomus* sp., *Sclerocystis* sp. and *Scutellospora* sp. The major bacterial groups are *Pseudomonas* sp., *Enterobacter* sp. and several gram-negative and gram-positive bacteria. In addition, many plant growth-promoting bacteria including *Azotobacter*, *Rhizobium*, *Pleomorphomonas diazotrophica*, *Bacillus megaterium* and *Bacillus thuringiensis* have been isolated from its rhizosphere. *J. curcas* can fix 5100–6100 kg C ha⁻¹ as biomass. Incorporation of *J. curcas* biomass into the soil results into significant increase in soil macro- and micronutrients. Keeping in view of the extent of microbial diversity in the rhizosphere of *J. curcas*, the basis of such microbial diversity is unclear. Further studies are required to link microbial diversity with the plant and environment. It is hypothesized that phyllospheric microbes might have significant role in framing the rhizosphere microbial community. To understand the plant-microbial interaction, this paper aims to address the diversity of phyllospheric microbes in different terrestrial plants and microbial species associated with the *J. curcas*.

20.2 Phyllosphere Environment and Microbial Diversity

The phyllosphere is a much intricate environment than the rhizosphere. It is a nutrient-poor environment for microbial activity compared to the belowground rhizosphere. The microbial colonization on leaves is not homogenous because leaf

veins, hairs and stomata affect surface uniformity. Microbial communities of phyllosphere are under constant variation of temperature, moisture and radiation over the day and night. These external factors also affect the phyllosphere microbiome by altering plant metabolism. Precipitation and wind also contribute to the temporal changes in the phyllospheric microbes.

There is limited information on the chemical characteristics of leaf surface that would explain for the high microbial activity. The unevenness of cuticle and complicated structures of veins and trichomes are the adverse structures for microbial growth. In addition, rain, dew and leaf exudates, pollutants and removal of nutrients after rain inhibit microbial proliferation. On the leaf surface, microorganisms assimilate carbon and nitrogen mainly from the leaf exudates. These organic compounds are generally glucose, sucrose and fructose. In addition to organic acids, alcohols and amino acids are also released from leaf. The concentration of the nutrients on the leaves is very low and occurs in the range of 1–20 $\mu\text{g/g}$ leaf. The analysis of protein and genomic data revealed that phyllospheric microorganisms assimilate plant-derived $\text{NH}_4\text{-N}$, amino acids and simple carbohydrates as primary N and C sources. Microbial stress response protein porins, the component of ATP-binding cassette transporters and TonB-dependent receptors, remain at high level among the phyllospheric microorganisms. This suggests that phyllosphere is a nutrient-poor environment for the growth of microorganisms.

The methylotroph species are generally found on the phyllosphere of many plants. These methylotroph species actively assimilate and metabolize methanol from plant pectin. Several phyllospheric microbial species have rhodopsins. These light-sensing proteins and proton pumps have different absorption spectra than the host plants. This indicates that energy metabolism of the phyllospheric microorganisms is not dependent on the plant. Phyllospheric microbes are capable of coping with UV radiation. These species possess pigments which help them to withstand UV radiations. A group of bacteria isolated from peanut produced pink or orange pigments when exposed to UV as protectant mechanism. Limitation of water and nutrients is compensated by microorganisms with the help of various mechanisms. Some epiphytic *Pseudomonas* sp. produces surfactants that increase the water retention ability of leaf surfaces. This increases solubilization and diffusion of nutrients for the microbial metabolism. Some bacteria increase the diffusion potential of the leaf cuticle by producing toxins. These toxins affect the ion transport potential of cell plasma membranes and improve water and nutrient availability for the phyllospheric microorganisms (Quigley and Gross 1994; Hutchison et al. 1995; Schreiber et al. 2005). Epiphytes also produce extracellular polysaccharides. These compounds protect the bacteria from water stress and help in binding to the leaf surface (Morris et al. 1997; Gal et al. 2003).

Using molecular techniques, phyllospheric microbial diversity has been studied. Microbial species richness on the phyllosphere is high in warmer and humid climates than the temperate regions. The alpha and gamma classes of *Proteobacteria* are the dominant bacterial phyla in phyllosphere. The *Bacteroidetes* and *Actinobacteria* represent the most common species of these phyla. The phyllosphere of several Mediterranean plants is dominated by lactic acid bacteria. In

summer, the most dominant species associated with these plants are *Firmicutes*. The growth of *Firmicutes* on the phyllosphere increases plant's tolerance to the hot and dry weather. At higher taxa level, phyllospheric microbiomes of different plants are similar, but at the species level, strains vary significantly. This suggests that bacterial diversity of the phyllosphere is linked with the micro-environment.

The environmental parameters like UV radiation, relative humidity and temperature influence the association of *E. coli* with plants (Seo and Matthews 2014). The indigenous phyllosphere microorganisms are also influenced by these environmental parameters. Changes in the indigenous microflora contribute to the promotion or prevention of *E. coli*. However, the role of the indigenous microorganisms on the long-term persistence of the pathogens is unclear. However, the interaction between pathogens and indigenous microbiota is difficult to understand because the diversity of phyllosphere microbiota varies with geographical locations and environment.

20.3 Ecological Niche of Phyllospheric Bacteria

In the phyllosphere, bacteria colonize typically as aggregates or clusters. In a study, it was found that up to 50 % of *Pseudomonas syringae* bacteria on bean leaves were present in clusters of 10^3 cells or more. It is assumed that before colonization, the incoming bacteria first reach at the leaf as single cells on different parts of the leaf. Only a few sites on the leaf are suitable for bacterial multiplication. The growth of cells in the favourable sites of leaf results into microbial colonies. Secondly, the bacterial species colonize on the leaf surface vary in their ability to produce offspring. This suggests that the leaf surface consists of sites with different conduciveness for bacterial cluster formation.

Moisture is one of the major factors that shape the bacterial clustering on leaf surfaces. Water stays for longer period in the veins and trichomes of leaf than other parts (Esser et al. 2015). Prolonged presence of water at these sites increases the nutrient availability. Most leaf nutrients available on the leaf surface are the photosynthetic compounds diffused from the leaf cuticle. Water droplets on a leaf surface also act as the effective sink for the diffused nutrients. The rate of diffusion of nutrients from leaf to water droplet depends on the volume of water and the activity of bacteria in consuming the nutrients. It also depends on the hydrophobicity and thickness of the cuticle (van der Wal et al. 2013). These factors regulate nutrient availability for bacterial community and act as the major driving factors for the spatial and temporal variation in bacterial population on the leaf surface.

20.4 Microbial Communities on the Phyllosphere

The phyllospheric microbial communities represent bacteria, filamentous fungi, yeasts, algae, protozoa and nematodes. Filamentous fungi are considered transient inhabitants of leaf surfaces because they are present predominantly as spores. However, the rapidly sporulating fungal species and yeasts colonize easily on the

leaf surface. Phyllospheric bacterial populations differ sharply among and within the same plant species. Bacterial population vary with the growth phase of the host plant as the plant's growth is associated with colonization of microorganisms. Variation in bacterial population in phyllosphere is caused by the extensive fluctuations in the physical and nutritional status of the phyllosphere. Plant species vary with different carrying capacity of the leaf microbiota. For example, the broader leaves of cucumber and beans carry high number of bacteria than grasses or waxy broad-leaf plants. The physicochemical environments of phyllosphere substantially cause variation in the bacterial flora.

The phyllosphere-dominating microorganisms are unique, but their community can be reproduced with the same plant system. However, the biogeography of these phyllospheric bacteria is less known. In a study, the bacterial communities on the leaves of *Magnolia grandiflora* were analysed by sequencing the 16S ribosomal RNA (rRNA) gene. Bacterial assemblages were dominated by members of the *Alphaproteobacteria*, *Bacteroidetes* and *Acidobacteria*. Patterns in community composition are measured by both relative abundance and Jaccard metrics. Distance based on the analyses indicated that trees positioned closely had more similar bacterial communities than the distantly placed. Indirect gradient analyses indicated that environmental parameters like canopy cover, slope, elevation and aspect of the ground beneath trees significantly influence bacterial community (Finkel et al. 2012).

20.5 Phyllospheric Microbes and Plant Growth-Promoting Activities

Generally it is considered that the community composition of phyllospheric microbes to some extent is random. It is the plant who selects microbes by providing favourable environment in the rhizosphere or phyllosphere for the specific microbial communities. Phyllosphere microbial communities influence plant growth. These microbial communities also contribute to the ecosystem function. However, the host plant is mainly responsible to modulate the plant-microbial interaction. Environmental factors also affect biosynthesis of many photosynthates within the plants. This change in metabolite concentration in plant affects the association of the rhizospheric microbes and alters plant development. Occurrence of certain microbial groups on the leaves suppresses feeding by insect larvae. Some signal molecules produced by phyllospheric microorganisms enhances plant growth under abiotic stress. For instance, the phytomicrobiome of *Arabidopsis* senses drought to maintain growth.

Many phylloplane-inhabiting microbes produce phytohormones. Among different phytohormones, auxin is the most commonly found molecule in the phylloplane. Like phyllospheric microorganisms belowground, PGPRs also produce auxin. This phytohormone plays an important role in the development of root system and overall plant growth. Indole acetic acid (IAA), another potential phytohormone, is also produced by the phyllospheric microorganisms. Many of these

phytohormones stimulate root growth that eventually enhances plant's root contact surface with soil and increases nutrient uptake. Due to this ability, microbial inoculants are recommended as a substitute or supplement for chemical fertilizers.

Yeasts are also widely distributed in the nature and coexist with other microorganisms. In a study, 12 yeast strains were isolated from leaf samples of a carnivorous plant *Drosera indica* L. This plant is currently endangered because of restricted habitats and use in herbal industries. The 16S rRNA gene sequence revealed that these yeasts belong to the phylum *Ascomycota* and *Basidiomycota*. The isolated yeasts produced indole-3-acetic acid (IAA). The IAA produced by wild yeasts modifies auxin-inducible gene expression in *Arabidopsis*. Phyllospheric yeasts can promote plant growth and may be considered for inclusion into biofertilizer for sustainable agriculture.

20.6 Phyllospheric Microbes and Plant Protection

Generally plants are exposed to the attack of herbivorous insects and pathogens. Herbivorous insects induce production of phytohormone jasmonic acid in plant, while many phyllospheric bacteria induce salicylic acid production in the host plant. The proportion of the two phytochemicals decides whether a plant would be susceptible or resistant against the pathogens. In an experiment, the bittercress plant (*Cardamine cordifolia*, Brassicaceae) was applied with jasmonic acid or salicylic acid prior to damage. Changes in abundance of phyllosphere bacteria were monitored to examine if chewing of herbivores correlates with the bacterial abundance on leaves. Study revealed that jasmonic acid treatment reduced herbivory, while salicylic acid treatment increased herbivory. Phyllospheric bacterial abundance was higher in herbivore-damaged plants than the undamaged plants. It is hypothesized that the abundance and the complex diversity of phyllospheric microorganisms have significant role in the plant's defence mechanism.

The phyllosphere acts as a media that supports the survival or proliferation of diverse microorganisms that are epiphytes, saprophytes and pathogens. Some phyllospheric microorganisms complete their life cycle along with the plant's growth. On the contrary, pathogens enter the leaf and multiply in the interior leaf tissue. Natural surface openings, such as stomata, are important entry ports for microorganisms. Stomata are the key organ for water transpiration and gaseous exchange. This activity is important for plant's growth. Recent studies show that stomata can limit pathogen entry as part of the plant innate defence process. Some plant pathogens have developed counter defence system. For example, the plant pathogen *Pseudomonas syringae* produces coronatine which suppress plant's stomata-based defence system.

20.7 Quorum Sensing in Phyllosphere

The microbial community dynamics of phyllosphere is complex. Cross talk or signal exchange occurs among the various microbial groups present on the phyllosphere. These signals regulate activities and community dynamics of various

phyllospheric microbial groups. These signals either help the plants to initiate immune responses to the harmful pathogens or facilitate the entry of beneficial microbes (Hartmann et al. 2015). Some *Bacillus* sp. secretes antibiotic in the presence of plant root exudates. This process keeps off pathogens in the rhizosphere. Phyllospheric bacteria also interfere with signalling between plants and microbial strains. Lipo-chito-oligosaccharides produced by many microorganisms are cleaved by certain bacteria which produce chitinases. In this way, these bacteria interfere with plant-microbial interaction. Plant signalling compounds are carbohydrates, proteins, organic acids or the secondary metabolites like flavonoids, phenol, phytohormones etc. The PGPR-related signalling compounds are phytohormones, acyl homoserine lactones, phenols and peptides.

Like other ecological niches, bacteria in the phyllosphere communicate by quorum sensing. One of the best studied quorum-sensing molecules is *N*-acyl homoserine lactone. These molecules trigger immune responses and change the phytohormone profile of plants. Plants also detect signal molecules from pathogens and respond by activating their own defence systems. Aboveground microorganisms communicate with the belowground microorganisms and shape plant's microbiomes. It has been observed that change in aboveground microbial communities due to environmental factor or even herbivore activity alters microbial community composition of the below ground.

20.8 Phyllosphere Microbial Diversity of *J. curcas*

Bioenergy crop *J. curcas* is a renewable energy plant. In a study the diversity of bacteria prevalent in phylloplane and rhizosphere of *J. curcas* compared. The diversity of bacterial 16S rRNA gene was estimated by molecular technique known as terminal restriction fragment length polymorphism (T-RFLP). The terminal restriction fragments (ribotypes) obtained from both rhizosphere and phylloplane were affiliated to *Firmicutes*, *Actinobacteria*, *Bacillus*, *Chloroflexi*, *Acidobacteria*, *Verrucomicrobia* and *Methylobacteria*. Fluorescence intensity of TRFs was high in the phylloplane than the rhizospheric soil. The ribotypes TRF56, TRF65, TRF95 and TRF423 were the main variables in soil. The ribotypes TRF466, TRF475 and TRF483 were major TRFs in the phylloplane of *J. curcas*. Diversity indices were high in soil than phylloplane. Study indicated that both belowground and aboveground plant parts harbour selective bacterial groups with different level of diversity and abundance. In a study, it was observed that *Jatropha* plantation increased the members of *Proteobacteria* and *Bacteroidetes* compared to unplanted soil (Agarwal et al. 2015). Several diazotrophic bacterial species, like *Azospirillum*, *Herbaspirillum*, *Burkholderia* and *Gluconacetobacter*, are present in the rhizosphere of *J. curcas* (Zehr 2011). These PGPRs occur on the rhizoplane or as endophytes. Some of these PGPRs fix nitrogen and promotes plant growth (Liu et al. 2011). These strains have the ability to enhance *J. curcas* through the production of IAA, solubilize inorganic P and produce ACC-deaminase and siderophore (Jha and Saraf 2012).

Phylloplane of *J. curcas* possesses many gram-positive and gram-negative bacteria. Plants like *Mangifera indica* have more of gram-positive *Bacillus* sp. and *Corynebacterium* sp. than gram-negative bacteria (Jager et al. 2001). Gram-positive *Bacillus* sp. has been isolated from leaves of groundnut, and these strains stimulate plant growth when inoculated as seed coat (Kishore et al. 2005). Methylophages are found from the phylloplane of *J. curcas*. Many species of *Methylobacteria* colonize plants as epiphytes and endophytes (Kwak et al. 2014; Dourado et al. 2015). *Methylobacterium* has been isolated from bamboo phylloplane (Madhaiyan and Poonguzhali 2014). These methylophages use methanol as C source released by the plant during pectin demethylation process (Galbally and Kirstine 2002). These bacteria can also multiply using other simpler photosynthates (Iguchi et al. 2015).

The role of phyllospheric microbes and their interaction with the growth of *J. curcas* is not clearly known. In an experiment, the dominant phylloplane bacteria of *J. curcas* were isolated, and their plant growth-promoting activities were evaluated. The 16S rRNA gene sequences of these bacteria were similar to *Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria*, *Firmicutes* and *Actinobacteria*. Most of the isolates were motile and gram variable. Many novel species closely related to *Ralstonia*, *Methylobacter* and *Actinomycetes* detected. The isolates exhibited PGPR activities like ACC-deaminase, phosphatase, K solubilization and indole acetic acid (IAA) production activity. These isolates were further tested on maize plants to check their plant growth-promoting activities. The isolates significantly increased the shoot and root length of the maize seedlings. Linear regression model of the PGPR activities significantly correlated with growth parameters. Among the plant growth-promoting attributes, ACC-deaminase and IAA production were the major growth factors for improving the maize growth.

In *J. curcas* phylloplane, the most abundant species were *Firmicutes*, *Alphaproteobacteria*, *Gammaproteobacteria* and *Actinobacteria*. Species belonging to *Betaproteobacteria* were the least abundant. The 16S rRNA gene sequences of the *Alphaproteobacteria* were similar to *Brevibacterium* sp., *Methylobacterium extorquens* and *Agrobacterium tumefaciens*. Phylloplane of many terrestrial plants contains *Alphaproteobacteria*. Some of these plants are *Magnolia grandiflora*, *Prunus* species and bamboo. *Firmicutes* are predominant on the phylloplane of plum and dessert plants. *Actinobacteria* are a group of important plant-associated spore-forming bacteria, known for their role in the biocontrol of pathogens, plant growth promotion and interaction with plants. *Actinobacteria* were mostly related to *Nocardia*, *Micrococcus*, *Brevibacterium* and *Agromyces*. This group has been found on the phylloplane of apricot (Jo et al. 2015) and many salt-tolerant plants (del Rocío Mora-Ruiz et al. 2015). *Gammaproteobacteria* has been found on the phylloplane of *Prunus* species (Jo et al. 2015) and dessert tree (Belkin and Qvit-Raz 2010). The isolates stimulated the growth of the maize seedling through various plant growth-promoting attributes. Such relation between PGPR activities of phylloplane microorganisms and plant growth has been found in agroforestry plants (George et al. 2002). Probably, the phosphates and indole acetic acid (IAA) production potential of the phylloplane bacteria stimulated plant growth. IAA stimulates cells present on root tip and shoot tip. Further studies are essential to explore the

phyllospheric microbes of *Jatropha curcas* to develop microbial inoculants for agriculturally important crops.

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