

Heading to the Origins – Rice Microbiome as Functional Extension of the Host

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Commentary Article

Plant has evolved along microbial symbionts, including bacteria, archaea, fungi, and protista. These symbionts, *i.e.* microorganisms living in close association with the host, with their collection of intricate genetic components have improved plant fitness by adding essential and functional capabilities. Therefore, one might continuously see plant as a superorganism composed of an amalgam of both selected symbiont microbiota and host cells. As single unit, both partners interact closely and often operate by complementarity of their metabolic capabilities. The nature of these interactions range from mutualism, where cooperation between symbionts evolved by enhancing all participants' inclusive fitness, to pathogenesis, where the symbiont increases its own growth and fitness selfishly, and trigger the host response leading to disease development and ultimately to terminate the interaction. Thus, plants have evolved to detect molecular patterns of symbionts and are capable to discriminate them by either reinforcement of beneficial cooperation [1] or sanctions of detrimental interactions [2].

Endophyte is a category of microbial symbionts that interacts intimately with the host cells. Endophytes ('endo', inside; 'phyte', plant) are mainly fungi and bacteria that thrive inside the host tissues and are detected in all vegetative stages of the host development. They invade the host plant from surrounding soil and are under direct influence of root exudates. Rice, as other plants, attracts distinct community of endophytes by releasing specific compounds into the soil [3]. A rich source of 'readily-available' (e.g. low molecular weight compounds) and recalcitrant nutrients diffuses into the rhizosphere (the soil which is directly affected by plant roots), attracting diverse heterotrophic microorganisms. Competent heterotrophic microorganisms first colonize the rhizoplane (*i.e.* the epidermal cells of plant roots) and later a selected fraction of these organisms may occupy the internal root tissues to become endophytic. Hence, most microbial colonization traits that are observed in rhizosphere are expected to be present in the endosphere [4]. Furthermore, microbes equipped with traits for efficient nutrient uptake, versatile nutrient metabolism, stress resistance and competitive fitness might be at an advantage to become endophytic. The rhizodeposition as mechanism of plant selection is poorly understood and further research is needed to clarify which molecules are discriminated by each microbe among the rich source of photo-assimilated compounds released by the host. Once inside the roots, endophytes might migrate to aerial tissues, including seeds [5,6]. Indeed, vertical transmission via seeds is another important mechanism for the establishment of endophytes. Various endophytes have been observed in rice seedlings growing aseptically [7-12] and it has been estimated that almost half of the early bacterial community from rice seedlings is originated from vertical transmission [9]. Thus, one might not exclude the selection of specific microbial communities to perpetuate mutualistic symbiosis [13]. The importance of vertical transmission becomes even more evident when beneficial endophytes improve host fitness upon adverse environmental conditions [14] or under conditions without induced stress [15].

A complete understanding of the community composition and

their putative functions inside the plant are necessary to foster the efficient use of endophytes as plant growth promoters. Many surveys of the prokaryotic community inside rice plants have been reported. For instance, culture-dependent and -independent surveys of the rice roots cv. APO identified an astonishing diversity of prokaryotic endophytes that were encompassed by 16 phyla/classes [16]. In both approaches, members of *Gammaproteobacteria* were the most abundant class, followed by *Alphaproteobacteria*. Members of *Epsilon-* and *Delta-proteobacteria*, *Bacteroidetes*, *Fibrobacteres*, *Planctomycetes*, *Nitrospirae*, *Tenericutes*, *Clostridia*, *Negativicutes*, candidatus division TM7, *Cyanobacteria* and *Crenarchaeota* were exclusively identified in the clones, whereas *Actinobacteria* were only found as isolates. Although diverse, the prokaryotic community was largely dominated (*i.e.* one third of the sequences) by members of the recently described genus *Kosakonia* [17]. The investigated *Kosakonia* strains revealed various *in vitro* plant growth-promoting properties such as production of siderophores, indole-3-acetic acid (IAA), acetoin and 1-aminocyclopropane-1-carboxylate (ACC) deaminase, solubilisation of inorganic phosphate, reduction of nitrate, and fixation of atmospheric N₂ as well as plant adaptation properties such as catalase production, oxidation of methanol, and production of extracellular cellulase, amylase and protease [17].

The first functional metagenome analysis from rice roots was carried out using the same cultivar described above. The results collected from the non-PCR-amplified DNA fragments also revealed high diversity of prokaryotic endophytes [18]. The identified genes encoding proteins suggest that the endophytic bacteria have special properties to live inside the host tissues, which often includes osmotic protection and resistance to oxidative stresses, production of hydrolytic enzymes and outer-membrane proteins involved in host recognition and adhesion, dedicated communication systems via autoinducer molecules, diverse transcriptional regulators to rapidly respond to host cues, metabolic adaptation to cope in oxic and anoxic niches, and degradation of aliphatic, aromatic and carbon storage compounds as well as ecological and nutritional versatility to use plant metabolites as carbon sources. In addition, many of the plant growth promotion properties described earlier and even more were detected in the rice metagenome [18]. The authors also showed that almost all enzymes involved in the N-cycle are represented in the endophyte metagenome. Genes encoding proteins

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for nitrification (occurring in aerobic condition), denitrification (anaerobic), and nitrogen fixation (semi-anaerobic) were detected in high abundance. Moreover, the *nifH* gene involved in nitrogen fixation was actively transcribed inside rice roots, suggesting that some bacterial species might contribute to the overall nitrogen pool inside the host [18-20]. This is an energetically highly demanding process, which only occurs when certain conditions are met. Under flood conditions and in the presence of reliable nutrient sources, qualified bacteria might actively incorporate atmospheric N₂ into the rice host metabolism, like rhizobia do inside leguminous plants.

Rice plants inoculated with endophytic bacteria show significant improvement in plant growth and grain yields. Vigorous seedling development is important for plant establishment and grain production and inoculation of rice seeds with endophytic bacteria *Herbaspirillum seropedicae*, *Simorhizobium meliloti*, *Achromobacter xylosoxidans*, *Pseudomonas* spp., *Sphingomonas trueperi*, and *Serratia marcescens* promotes seedlings' growth [21-26]. Nitrogen, one of the most limiting nutrients for rice cultivation, is also significantly increased inside rice plants inoculated with diazotrophic endophyte strains *Herbaspirillum seropedicae*, *Burkholderia* spp., *Rhizobium* sp. and *Corynebacterium* sp. as well as fungal endophytes *Phomopsis liquidambari* [22,25,27-29]. Increased in grain yields have been reported for rice plants inoculated with endophytes *Rhizobium leguminosarum* bv. *trifolii*, *Rhizobium* sp. IRBG74, *Burkholderia cepacia/vietnamiensis* complex, *Pseudomonas* sp., *Herbaspirillum seropedicae*, *Gluconacetobacter diazotrophicus*, *Azospirillum brasilense*, and *Pantoea agglomerans* strains [30-33]. Endophytes can also improve plant growth via biocontrol mechanisms. Those with excellent antagonistic properties against plant pathogens might be used to reduce pathogen growth. Rice endophytic bacteria *Acidovorax* sp. S20, *Acinetobacter baylyi*, *Acinetobacter calcoaceticus*, *Acinetobacter junii*, *Acinetobacter* sp. B, *Actinomyces* spp., *Agrobacterium larrymoorei*, *Agrobacterium radiobacter*, *Arthrobacter citreus*, *Bacillus amyloliquefaciens*, *Bacillus cereus*, *Bacillus megaterium*, *Bacillus mycoides*, *Bacillus polyfermenticus*, *Bacillus pumilus*, *Bacillus simplex*, *Bacillus* sp. WL-3, *Bacillus sphaericus*, *Bacillus subtilis*, *Brevibacillus brevis*, *Brevibacterium epidermidis*, *Burkholderia cepacia*, *Burkholderia gladioli*, *Burkholderia glumae*, *Burkholderia kururiensis*, *Burkholderia* sp. KJ006, *Curtobacterium flaccumfaciens*, *Deinococcus aquaticus*, *Enterobacter cloacae*, *Gluconacetobacter diazotrophicus*, *Klebsiella mobilis*, *Microbacterium esteroaromaticum*, *Micrococcus lylae*, *Paenibacillus cineris*, *Paenibacillus favisporus*, *Paenibacillus lentimorbus*, *Pantoea agglomerans*, *Pantoea ananatis*, *Pantoea dispersa*, *Pantoea stewartii*, *Pseudomonas aeruginosa*, *Pseudomonas entomophila*, *Pseudomonas fluorescens*, *Pseudomonas oryziphilus*, *Pseudomonas putida*, *Pseudomonas* sp. PALXIL12, *Pseudomonas stutzeri*, *Sphingomonas capsulate*, *Staphylococcus arlettae*, *Staphylococcus simulans*, *Stenotrophomonas maltophi*, and *Xanthomonas* sp. LMG 20137 and fungi *Fusarium moniliforme*, *Trichoderma*, *Harpophora oryzae*, *Phialemonium curvatum*, *Phaeosphaeriopsis musae* have been recommended for their biocontrol potential [7,34-43].

Until recently, microbial community detected inside the host plants has been associated with diseases development. We learned from human microbiome the importance of high diversity community to maintain the health and functioning stability. As in human microbiome, plant disease outbreaks are often associated with shifts of the whole microbial community originated from the imbalance growth of specific symbiont community. The symbionts mentioned above exemplify the importance of endophytes for the host fitness and grain production. It also demonstrates that host genome and its symbiont microbiome are intimately interconnected creating the rice holobiome,

the genome content of this superorganism. As the study of Gregor Johann Mendel on genetic inheritance in garden peas revolutionized biology by introducing the laws of inheritance, the concept of plant holobiome will allow us to understand even further the factors affecting plant production. Sustainable and responsible agricultural production will be guided by our knowledge on how plant holobiome operates.

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