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How do Plants-Having Different Exudation Patterns-Shape a Similar Microbial Community?

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Short Communication

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ABSTRACT

Microorganisms associated with plants have been shown to improve plant growth and yield participating in the biogeochemical cycles of elements in soil. For these reasons, the rhizosphere microbiome is considered one of the key determinants of plant health and productivity. Plants can influence the qualitative and quantitative composition of the rhizosphere microbial community by releasing different classes of organic compound. Yet, this release depends on several factors, such as plant genotype, soil properties, plant nutritional status, climatic conditions. Within a previous study, we showed that the rhizosphere microbial communities associated to both iron (Fe)-sufficient and Fe-deficient tomato and barley plants, grown in different agricultural calcareous soils, were surprisingly similar and formed by bacterial strains that exhibit plant growth-promoting (PGPR) traits.

In the present commentary, we evaluate the possible role of variables, as for instance nutrient starvation, which might induce shifts in the microbial community independently from the plant species. The exudome (i.e. rhizosphere organic compounds originating both from plants and microorganisms) has been proposed as tool to better understand the dynamics of the microbiota in the rhizosphere. Furthermore, we also discuss the advantages and drawbacks of the "OMICS" approaches (16S profiling, metagenomics and metatranscriptomics sequencing) used in the study of microbial communities. In conclusion, we suggest further milestones that need to be reached in order to develop efficient biofertilization practices for an integrated crop nutrient management.

The soil ecosystem and especially the rhizosphere compartment, i.e. the volume of soil influenced by root activities, is widely recognized as a habitat hosting highly diverse communities of living organisms within which bacteria represent the most abundant group, in terms of species diversity and community size [1]. Within natural, agricultural and forest soils, the rhizosphere is highly dynamic in terms of time and space housing a wide variety of complex biological and chemical reactions that are mainly driven by organic compounds released by plants [2]. These so called root exudates, including low molecular weight (LMW: organic acids, amino acids, sugars, phenolic acids, flavonoids, etc.) and high molecular weight (HMW: carbohydrates, enzymes, etc.) molecules, are especially triggered by biotic and/or abiotic stresses, such as nutrient deficiencies [3]. Within this ecological niche, soil microorganisms can be either attracted or repelled by root exudates, thus generating an uneven distribution of microbiota in the soil [4]. Moreover, several pieces of research have demonstrated that different plant species characterized by different qualitative and quantitative pattern of exudation might differently drive the shaping of their own rhizosphere microbiome [5-8].

In a recent paper, we analysed the rhizosphere microbial communities of both iron (Fe)-sufficient and Fe-deficient tomato and barley plants, grown in two different agricultural calcareous soil by a 454-pyrosequancing approach [9]. Tomato and barley plants rely on two different strategies to acquire Fe from the growth substrate, thus having also two different root exudation profiles. In particular, in the case of monocots (e.g. barley), the predominant class of organic compound released is composed of non-proteinogenic amino acids, known as phytosiderophores, whilst dicot plants (e.g. tomato) are known to exude mostly organic acids [10]. Surprisingly, in a very short time period (6 days of cultivation), these two plant species induced the selection of a similar microbial community formed by bacterial strains that most likely participate in the biogeochemical cycles of elements and that potentially exhibit plant growth-promoting (PGP) traits. This result is still more interesting considering that dicots (like tomato), differently from monocots, are able to acidify the rhizosphere as a consequence of the Fe shortage [11]. Therefore, these findings

suggest that evolutionary distinct plants might adopt different tools to reach the same goals (selection of similar microbiota aimed at coping with Fe starvation) [9]. However, do these observations reveal a general feature? Is this behaviour also adopted by other plant species and/or for other nutritional stresses in natural conditions (i.e. field)? Further studies considering a higher number of plant species and soils as well as time course experiment and field trials will contribute clarifying this point.

Several authors have postulated that in stressing environments, such as desert soils and hypersaline ponds, the rhizosphere effect (i.e. root exudation) might play a minor role in shaping the microbial community, which could be overridden by the "extreme" conditions (e.g. soil aridity, salinity) [12,13]. According to these observations, Fe deficiency might be envisaged as a harsh physiological condition acting through the plant, independently from the species, as a strong selective pressure on the soil microbiota. Indeed, such stress might induce the release of common exudates among different plant species that can constitute either positive signal(s), attracting and favouring the proliferation of useful microorganisms, or negative signal(s), repelling detrimental ones. This hypothesis further highlights the urgency of deciphering the plants exudome (i.e. qualitative and quantitative composition of root exudates) at high resolution to shed light on the possible effectors involved in the shift of the rhizosphere microbiome **(Figure 1).** In spite of the importance of this critical step, one of the major limitations in analyzing the plants exudome is the difficulty to collect adequate amounts of rhizosphere soil and to quantitatively recover exudates, especially in natural conditions and in field experiment. This kind of analyses are further complicated by the series of dynamic interactions occurring between exudates and the tripartite system root/microorganism/soil-minerals and that should also be considered [2,10]. Up to the now, the experimental designs aiming at studying the activity of root exudates, either on soil particles (e.g. nutrient cycling) or on microorganisms, represent a big challenge and very often simplifications of the systems are required, even though part of the information could inevitably be lost [14].

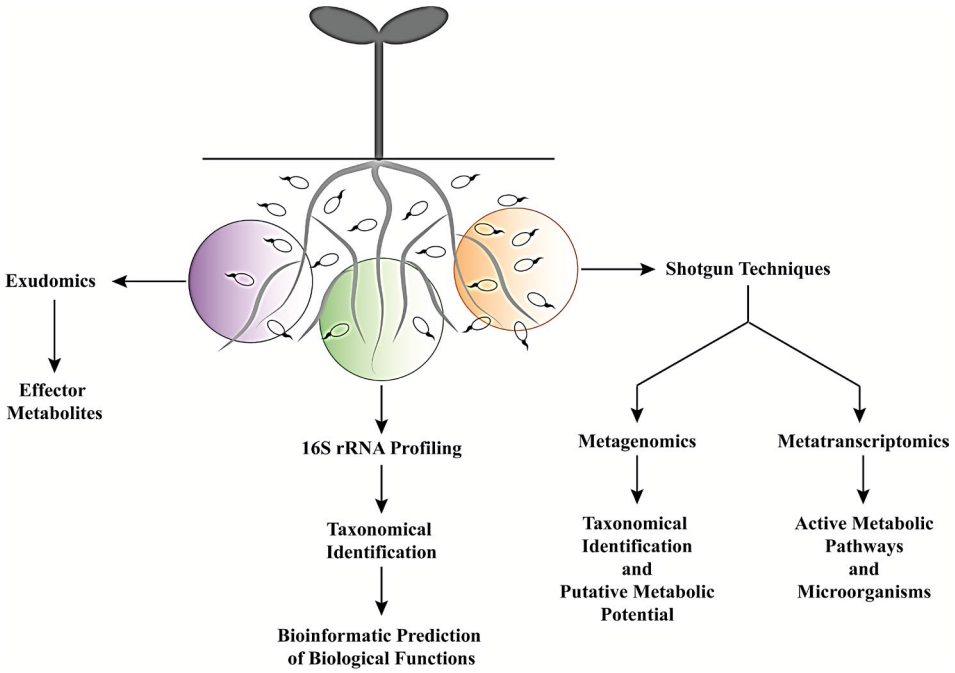

Figure 1. Schematic drawing of the different approaches applied to study the rhizosphere microbial community and its interaction with host plants. The picture reports also the expected outcome from the application of the different analytical techniques.

To date, the majority of the studies aiming at studying the composition of the soil microbial communities have been based on 16S rRNA profiling giving a taxonomical snapshot of the populations, in terms of relative abundance and diversity of bacteria and archea **(Figure 1)** [9,15-20]. To further implement the taxonomical description of a microbial population, bioinformatic tools, as for instance the algorithm PICRUSt, can be exploited to predict the community's putative functional capabilities on the base of *16SrRNA* gene [21]. Nonetheless, the information provided is still indirect evidence and this approach may fail in completely describing the functional diversity and the characterizing aspects of the plant-associated microbiome [22]. However, this approach does not consider the horizontal gene transfer where genes integrated in different mobile genetic elements (plasmids, integrons and transposons) can be disseminated and transferred among bacteria, even taxonomically distant ones. Briefly, bacteria of different species, sharing a common environment can acquire or lose some metabolic functionality, even in a relatively short time [23]. This is particularly true in highly competitive environments, hotspots like the rhizosphere, and stressing environments. To overcome the problem on the functional uncertainty of the bacterial communities *in situ*, other approaches including the metagenomic sequencing are more promising. The progressive reduction of sequencing costs has made the application of shotgun sequencing (metagenomics and metatranscriptomics) more attractive and more feasible. In a typical shotgun metagenomic approach, the whole DNA present in a given environment is sequenced allowing the determination of the functional potential encoded by the microbiome as well as the discovery of novel enzymatic activity [24,25]. At the moment, the deeper insight in the microbiome functionality is given by the shotgun metatranscriptomics approach, which, through the sequencing of the whole

RNA, aims at detecting those genes that are actively expressed and thus giving the possibility to gain useful knowledge about the metabolic processes that take place *in situ* [26]. Comparative analyses of metagenomic datasets may provide further information about both diversity and functionality of rhizobacterial communities [27].

At systemic level, the combination of metagenomic, metatranscriptomic and exudomic analyses will allow a deeper understanding of the molecular interactions both between soil microbiota and between microorganisms and their host plants. These data will also earn potential genes, biochemical pathways and metabolites that might play a paramount role in the plant mineral nutrient dynamics within the rhizosphere and in the functionality of nutrient acquisition mechanisms in roots.

The influence of the rhizosphere microbiome on plant mineral nutrition is even more important considering the current need to increase staple food production yet reducing the exogenous inputs, like fertilizers. Modern agriculture aims towards more sustainable practices, possibly based on the co-application of chemical fertilizers and PGPR strains (i.e. integrated nutrient management) [28]. In this scenario, the autochthonous microflora might outcompete with exogenous biofertilizing bacteria, thus possibly vanishing their beneficial effects. Does it really occur? And then, to which extent does this interaction depend on the buffering potential of the autochthonous community? Nevertheless, there still is a gap of knowledge on this topic. Therefore, it is advisable that future studies concerning the development of biofertilzer cocktails include and focus on these crucial aspects. However, the applicability of biofertilizers and their effectiveness require necessarily knowing the exudome, considering its driving role in shaping the rhizosphere microbiome.

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