Indian J. Plant Genet. Resour. 35(3): 360–364 (2022)
DOI 10.5958/0976-1926.2022.00100.0

Interlinking Soil Microbial Diversity and Rhizodeposition for Enhancing Nutrient Uptake and Productivity

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To provide sufficient food and nutrition to an estimated world population of 9.6 billion by 2050, the present level of global food production has to be increased by 50-70%. This monumental task will be abysmally difficult to achieve, owing to the reduction in arable land, increase in frequency and intensity of climate extremes, shrinkage in available agricultural inputs, reduction in soil fertility and organic carbon, predicted inundation of coastal ecosystems due to ingression of seawater, reduction in the diversity of plants due to rapid afforestation, the incidence of newer pests and diseases, etc. Plant species allow specific groups of microorganisms to proliferate in the rhizosphere, depending upon the qualitative and quantitative nature of photo-assimilated carbon flow in the subterranean system in the form of rhizo deposition, the primary source of food and nutrition to the growing organisms. Thus, the quality and quantity of rhizodepositionin a crop ecosystem will determine the diversity of crop-associated rhizosphere microbes vis-à-vis the fate of biogeochemical cycles operating in the rhizosphere, and the availability of essential nutrients for the growing crops to realize genetic yield potential. Therefore, enhancing and or altering the structural and functional diversity of beneficial microbes in the rhizosphere by changing the nature of photo-assimilated carbon in rhizodeposition, quantitatively and qualitatively, through genetic augmentation of crop plants, would facilitate the identification of superior plant varieties for a given ecosystem for ensuring improved plant growth and yield by enhanced nutrient availability.

Introduction

One of the influencing factors that determine the composition of rhizomicrobiome is the composition of rhizodeposition, the primary source of food and nutrition for organisms to proliferate (Tian *et al*., 2019) in the rhizosphere. The translocation and release of photo-assimilated carbon, entrapping solar energy, water and carbon dioxide, from plant roots into its surroundings is called rhizodeposition, which is composed of root-released tissue cells, sloughed-off cells, mucilages, exudates, lysates, volatile compounds, etc., individually called rhizodeposits. The composition of rhizodeposits varies from pant to plant and within the plant varieties grown in different climatic conditions, quantitatively and qualitatively. Among the rhizodeposits, root exudates are the most dynamic and versatile and the quality and quantity of which vary with plant types and soil, environment, and age of the plants (Crowley and Rengel, 1999). That is why the rhizomicrobiome of rice is different from that of maize, groundnut, soybean, pigeon pea, etc., and even within rice varieties grown in India and Japan. The root exudates include organic compounds (carboxylate anions, phenolics, carbohydrates, amino acids, enzymes, proteins, organic acids, etc.) and inorganic ions (protons, phosphate, and other nutrients, etc.) (Dakora and Philips, 2002; Bias *et al*., 2004), the composition of which will vary from plant to plant (Table 1). Though the quantitative and qualitative nature of root exudates significantly influence the functional and structural diversity of microbes in the rhizosphere, other rhizodeposits also play significant roles in disease suppression, production of antimicrobial agents, and messenger molecules for communication, etc. The final product of the rhizodeposition, after microbial utilization, is the soil organic carbon, the composition of which will be determined by the composition of rhizodeposition (Villarino *et al*., 2021). As soil organic matter content is the indicator of soil health, the composition of rhizodeposition vis-à-vis the composition of soil organic matter will influence the status of soil health. Depending upon the plant species and age of the plant, 20-50% of photo-assimilated carbon is distributed to the roots (Johnson *et al*. 2006)) to sustain the subterranean system. For example, in cereal crops, 50% of the 50% photo-assimilated carbon is required for root respiration and biomass and the rest 50% meant for root rhizodeposition (Fig. 1). However, in legumes, the situation is little different considering the fact that

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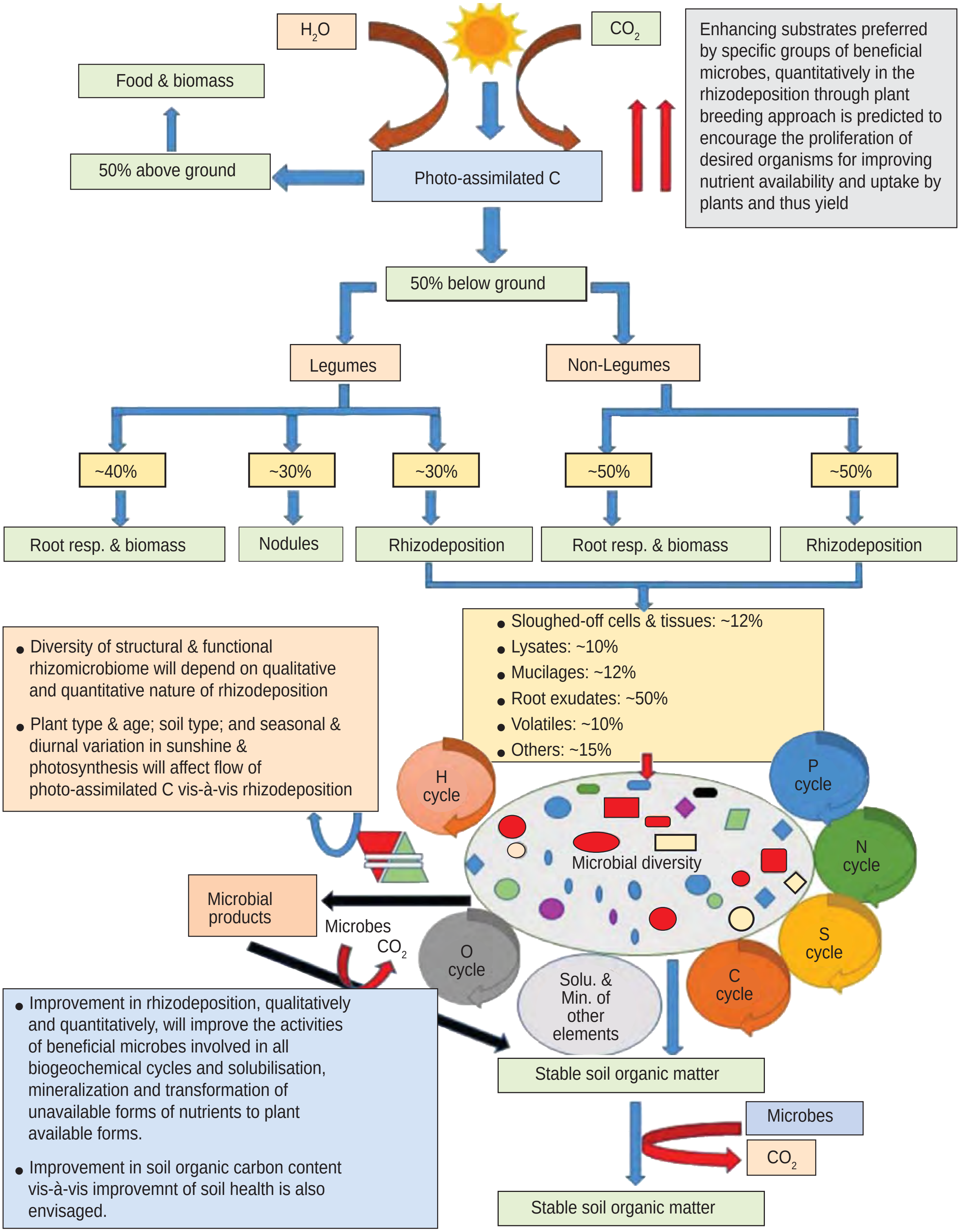
Table 1. Composition of root exudates of different plant species (peanut, rape, tomato, flax, etc.) that shape the beneficial microbial dynamics in the rhizosphere

Exudate component	Rhizosphere function	Compounds identified in root exudates	Reference
Organic Acids	Nutrient source, chemo-attractants, chelators, etc.	Citric, oxalic, malic, fumaric, succinic,, acetic, butyric, formic, lactic, malonic, glutaric, rosmarinic, vanillic, etc.	Dakora and Philips (2002); Nguyen (2003), Bias *et al.* (2004)
Amino acids	Nutrient source, chemo-attractants, chelators, etc.	Alanine, asparagine, aspartate, cystein, cystine, glutamate, glycine, lysine, methionine, serine, threonine, proline, tryptophan, arginine, etc.	
Sugars & Vitamins	Promoters of plant and microbial growth, nutrient source, etc.	Glucose, fructose, galactose, maltose, ribose, xylose, rhamnose, arabinose, raffinose, deoxyribose, oligosaccharides, biotin, thiamin, niacin, pantohenate, riboflavin, etc.	
Enzymes	Catalyst for P release from organic molecules, biocatalyst for organic matter transformation, etc.	Acid/alkaline phosphatase, invertase, amylase, protease, etc.	
Purines	Nutrient source	Adenine, guanine, cytidine, uridine	
Inorganic ions and gases	Chemoattractant signals to microbes	HCO_3^-, OH^-, H^+, CO_2, H_2, etc.	
Phenolics	Nutrient source, chemo attractant signals to microbes, microbial growth promoters, nod gene inducer/ inhibitors, chetalors, phytoalexins, etc.	Liquiritigenin, diadzein, genistein, coumetrol, eriodictyol, naringenin, isoliquiritigenin, umbelliferone, formonoetin, quercetin, leteolin, 4',7-dihydroxyflavone and derivatives, chalcone, etc.	
Root border cells	Produce signals that control mitosis, produces signals, stimulate microbial growth, release chemo-attractants, synthesize defense molecule, etc.		

30% of the 50% photo-assimilated carbon is required for sustaining root nodules and nitrogen fixation (Fig 1) and the rest 40% and 30% will be recruited for sustaining root respiration and biomass and rhizodeposition, respectively. Given that nearly 50% of photo-assimilated carbon is required to sustain a subterranean system, tailoring the rhizodeposition, qualitatively and quantitatively, will be pivotal in changing the structural and functional dynamics of microbial profile in soil for enhancing the nutrient availability and uptake for sustainable food production in future.

How Rhizodeposition Influences Microbial Diversity

Plants translocate an array of photo-assimilated carbon to sustain the subterranean system including root respiration and biomass gain and rhizodeposition. The dynamics of structural and functional diversity of microbial community play the most important role in nutrient mobilization, availability and subsequent uptake by the plants from the limited available pool of nutrients in the soil and thus influencing the plant growth and yield. As rhizodeposits, particularly root exudates, are primary substrates for the proliferation of different microorganisms in the rhizosphere, enhanced flow of photo-assimilated carbon (Fig. 1) in the form of root exudates and its differential composition, qualitatively and quantitatively, will play a pivotal role in influencing the structural and functional beneficial microbial community in the rhizosphere vis-à-vis nutrient availability. Suppose enhanced exudation of organic acids is targeted by genetic augmentation in the varietal development programme, there will be likely an enhancement in the solubilisation and availability of non-available forms of nutrients directly or indirectly. Directly by mineralization and indirectly by enhancing the population of microbes which are capable of utilizing organic acids as primary sources of substrates for growth and multiplication, thereby enhancing the solubilisation of essential elements from unavailable to available forms. Similarly, enhanced exudation of monosaccharides will encourage rapid multiplication of microbes than exudation of oligo- and poly-saccharides. Enhanced exudation of acid/alkaline phosphatase by a particular crop variety will enhance the availability of inorganic phosphate than the variety which exudates out fewer phosphatases (Fig. 1). The same is true for all other rhizodeposits in different manners. Therefore, enhancing the quantity of preferred substrates in the root exudates, by genetic augmentation, for a desired beneficial group of microorganisms involved in different biogeochemical cycles would have the potential to



Enhancing substrates preferred by specific groups of beneficial microbes, quantitatively in the rhizodeposition through plant breeding approach is predicted to encourage the proliferation of desired organisms for improving nutrient availability and uptake by plants and thus yield

- Diversity of structural & functional rhizomicrobiome will depend on qualitative and quantitative nature of rhizodeposition
- Plant type & age; soil type; and seasonal & diurnal variation in sunshine & photosynthesis will affect flow of photo-assimilated C vis-à-vis rhizodeposition

- Improvement in rhizodeposition, qualitatively and quantitatively, will improve the activities of beneficial microbes involved in all biogeochemical cycles and solubilisation, mineralization and transformation of unavailable forms of nutrients to plant available forms.
- Improvement in soil organic carbon content vis-à-vis improvemnt of soil health is also envisaged.

Fig. 1. Predicted fate of photo-assimilated carbon and possible role of rhizodeposition in nutrient dynamics and soil organic matter content

alter the patterns of nutrient mobilization, and disease suppression, and other vital soil processes defining outcome of plant-microbe interaction. Because of the flow of photo-assimilated carbon, the rhizosphere is abundant in various nutrients due to an aggregation of root exudates (Dakora and Philips, 2002) including amino acids, sugars, organic acids, vitamins, and enzymes (Bias *et al*. 2004, Gray and Smith, 2005) (Table 1). Root exudates not only function as a source of food but also function as repellents against pathogens and as attractants that aggregate beneficial microbes (Ahemad and Kibert, 2014, Hassan *et al*., 2019). However, the flow of carbon in the rhizospherevaries with the physiological status, species of plants, and microorganisms that can be present in a given environment (Kang *et al*., 2010).It has also been reported that soybean root exudates trigger an early symbiotic association between *Bacillus diazoefficiens* and soybean and also act as a messenger (Liu *et al*., 2015, Walker *et al*., 2004). Therefore, for shaping the rhizosphere interaction and its beneficial outcome, the root exudates play a crucial role. The classification and functions of root exudates are shown in Table 1.

Therefore, the population dynamics of predominant genera (*Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcous*, *Pseudomonas*, *Serratia*, *Cellulomonas*, *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Mesorhizobium*, *Rhizobium*, *Pantoea*, *Methylobacterium*, *Exiguobacterium*, *Paenibacillus*, *Azoarcus*, *Azospirillum*, *Alcaligenes Streptomyces*, *Streptosporangium*, *Thermobifida*, *Micromonospora*, etc.) of bacteria and actinomycetes, representing plant growth-promoting group, will be determined by the quality and quantity of rhizodeposition, preferably root exudates as described above, from the flow of photo-assimilated carbon into the subterranean system. In turn, the dynamics of the above microflora will influence the availability of nutrients for the plant to take up for influencing the yield.

Future Perspective and Action Points

The genetic yield potential of any crop variety can only be realized with the favourable environmental condition along with the availability of essential nutrients. As such the availability of nutrients will be the outcome of the interaction of functional diversity of the microbes and bio-geochemical cycles and transformation and mineralization processes in the soil. Keeping other factors constant, the qualitative and quantitative nature of rhizodeposition will be the determinant of the structural and functional diversity of the rhizomicrobiome. However, to understand the roles of rhizodeposition in influencing the rhizomicrobiome vis-à-vis availability of essential nutrients for realizing the genetic yield potential of crops, a culture-independent approach would be required along with complete profiling of rhizodeposition using omics approaches. However, all these approaches are in their infancy. As there is much variability among the wheat genotypes in root growth rates, exudates, and responses to the structural and functional microflora of un-ploughed soil, there is probably a lot of variation in rhizodeposition patterns among different plant species and that is the reason why there is wide variation in microbial profiles across different crop species. Therefore, it is possible to alter the dynamics of beneficial microbes in the rhizosphere by altering the photo-assimilated carbon flow through breeding processes. However, technological innovations are required to quantitatively and qualitatively assess both the flow of carbon as well as a shift in community structure during the augmentation of the genetic makeup of the plant. Therefore, for future agriculture to flourish in the increasingly parched planet to produce sufficient food for all in the backdrop of dwindling land, inputs and adverse climatic factors, the focus should be diverted to harness most from the interaction of photo-assimilated carbon flow-rhizodeposition-rhizomicrobiome in a given production system.

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