frontiers in
PLANT SCIENCE

HYPOTHESIS AND THEORY ARTICLE
published: 14 June 2013
doi: 10.3389/fpls.2013.00188

Buffet hypothesis for microbial nutrition at the rhizosphere

*Martha G. López-Guerrero, Ernesto Ormeño-Orrillo, Mónica Rosenblueth, Julio Martinez-Romero and Esperanza Martínez-Romero**

Centro de Ciencias Genómicas, Universidad Nacional Autónoma de México, Cuernavaca, Mexico

Edited by:
Boris Rewald, University of Natural Resources and Life Sciences, Austria

Reviewed by:
Ivika Ostonen, University of Tartu, Estonia
Catharina Meinen, Georg-August-Universität Göttingen, Germany

****Correspondence:***
Esperanza Martínez-Romero, Centro de Ciencias Genómicas, Universidad Nacional Autónoma de México, Avenida Universidad SN, Cuernavaca, Morelos CP 62210, Mexico
e-mail: emartine@ccg.unam.mx, esperanzaeriksson@yahoo.com.mx

An emphasis is made on the diversity of nutrients that rhizosphere bacteria may encounter derived from roots, soil, decaying organic matter, seeds, or the microbial community. This nutrient diversity may be considered analogous to a buffet and is contrasting to the hypothesis of oligotrophy at the rhizosphere. Different rhizosphere bacteria may have preferences for some substrates and this would allow a complex community to be established at the rhizosphere. To profit from diverse nutrients, root-associated bacteria should have large degrading capabilities and many transporters (seemingly inducible) that may be encoded in a significant proportion of the large genomes that root-associated bacteria have. Rhizosphere microbes may have a tendency to evolve toward generalists. We propose that many genes with unknown function may encode enzymes that participate in degrading diverse rhizosphere substrates. Knowledge of bacterial genes required for nutrition at the rhizosphere will help to make better use of bacteria as plant-growth promoters in agriculture.

Keywords: rhizosphere, speciation, root exudates, soil microbiology, bacterial genomes

INTRODUCTION

Ecophysiology of root systems cannot be understood without the microbiota that colonize outside and inside roots. Bacteria and fungi may impact root physiology, produce hormones, stimulate root growth or alter its morphology. Microbes provide protection against pathogens, tolerance to abiotic stresses, resistance to insect or herbivore attack; even allelopathy may be due to root-associated microorganisms. An extensive review on the ecophysiological contributions of microorganisms to plants has been published (Friesen et al., 2011) and reviews on rhizospheric bacteria also highlight their effects on plants (van Loon et al., 1998; Bais et al., 2006; de Bruijn, 2013). Microbial endophytes (meaning residing inside the roots) may contribute to nutrient assimilation and other plant traits, however, they are normally in lower numbers than rhizospheric bacteria (Rosenblueth and Martínez-Romero, 2006; Hirsch and Mauchline, 2012) and we will focus only on the latter. Over the years, studies on root microbiota have addressed several questions such as: How are microbes selected or maintained in roots? What are the sources and resources for root microbes? How do bacteria or fungi affect root physiology? Are there key species that have a larger impact on plants? Is nutrient competition driving bacterial evolution? There are still questions without answer.

The term rhizosphere was proposed by Hiltner (1904) and refers to 1–7 mm of soil from the root surface. The rhizosphere effect is the enrichment of microbial populations at the root–soil interface. Outside roots there is a heavy colonization of bacteria (for example, 10^9 *Rhizobium phaseoli* cells per gram of fresh maize root; Gutiérrez-Zamora and Martínez-Romero, 2001) mainly stimulated by root-derived nutrients. The microbial community itself may modify root nutrients and may contribute with resources by transforming soil material (Baelum et al., 2008), by fixing nitrogen (Fischer et al., 2012) or producing vitamins (Phillips et al., 1999; Ramírez-Puebla et al., 2013). Rhizosphere nutrients may be very variable depending on the plant (Brown et al., 2008; Haichar et al., 2008; Badri et al., 2013) and the soil biotic and abiotic conditions. There are bacterial species commonly encountered as rhizosphere colonizers but each plant species may harbor particular microbes at the rhizosphere (Lundberg et al., 2012). A complex rhizosphere community may be structured in relation to the microbial specialization for different nutrients. The diversity of nutrients available at the rhizosphere may be equated to a buffet, and distinct microbes may have preferences for some of them. Furthermore, we propose that a large proportion of products from genes highly expressed by bacteria at the rhizosphere are involved in the transport and catabolism of the various buffet entries.

PLANT-DERIVED NUTRIENTS AT THE RHIZOSPHERE

Plants may be considered as a growth media for their microbiota (Brown et al., 2008). Root exudates determine bacterial community structure (Haichar et al., 2008) and rhizodeposits (Dennis et al., 2010) may do the same as well. Root exudates contain a large diversity of molecules (reviewed in Walker et al., 2003; Bais et al., 2006; Dennis et al., 2010; Ramírez-Puebla et al., 2013) and around 10,000 types of flavonoids are known from plants (Ferrer et al., 2008). Additionally, arabinogalactan-proteins (AGPs) that have a large proportion of carbohydrates covalently bound to polypeptides are found abundantly in exudates (Fincher et al., 1983). AGPs are considered the most structurally complex molecules in nature (Majewska-Sawka and Nothnagel, 2000).

Exudates and other plant substances may act to select microorganisms (Walker et al., 2003; Shaw et al., 2006; Badri and Vivanco, 2009; Dennis et al., 2010; Berendsen et al., 2012) as prebiotics do (Ramírez-Puebla et al., 2013); additionally, just adhesion to plant lignocellulose acts to select bacteria from the soil (Bulgarelli et al., 2012). From root extracts, the phenolic fraction was found to have an important role in conditioning bacterial communities (Badri et al., 2013). Roots have a remarkable ability to synthesize diverse secondary metabolites (Flores et al., 1999) and many complex carbon molecules (Dennis et al., 2010; Mathesius and Watt, 2011). Seeds are also a source of nutrients for plant-associated bacteria and some contain large amounts of phytate (Lott et al., 2000). Germinated seedlings provide enough sulfur in root exudates for bacterial growth (Snoeck et al., 2003).

Plants may control bacterial growth with antimicrobials such as phytoalexins (González-Pasayo and Martínez-Romero, 2000; Shaw et al., 2006), bacterial-quorum plant-produced mimics (Bauer and Robinson, 2002), or other substances yet unknown. Additionally, plant-derived substances may control bacterial metabolism (Shaw et al., 2006; Hassan and Mathesius, 2012), perhaps to the plant own benefit. On roots, bacteria exhibit a differential gene expression that varies depending on the plant (Ramachandran et al., 2011; López-Guerrero et al., 2012). The analysis of known bacterial genes expressed in the root or rhizosphere may help us deduce conditions therein. Based on the large numbers of transporters expressed by rhizospheric bacteria (Ramachandran et al., 2011; López-Guerrero et al., 2012), we propose that each bacterial species can use a wide range of the nutrients that plants provide from roots.

Root-derived nutrients may be modified by the associated microbiota directly by transforming them to new substances (Shaw et al., 2006) or by inducing changes in plant production of exudates from the interaction with the plant. Symbiosis with microbes and fungi can alter the composition of exudates (Bais et al., 2006; Scheffknecht et al., 2006).

SOIL-DERIVED NUTRIENTS

Besides root-derived nutrients, microbes at the rhizosphere may profit from soil-derived substrates. Many soils are substrate rich especially those having high content of organic matter, not even considering man-derived soil contaminants. Soil has perhaps the highest microbial diversity of all habitats. This may be explained by soil structure, diverse soil physical characteristics, differences in pH, minerals, metals, plethora of soil microhabitats but also by an unknown large diversity of natural substances found in soil. Humic acids in soils are very complex and their diverse chemical structure has just started to be determined (Nebbioso and Piccolo, 2001). In the rhizosphere different Amadori compounds (N-glycosylamines) may be found that form spontaneously from decomposing plant material or by *Agrobacterium* spp. (Baek et al., 2003).

Soil is not only the depositary of plant and animal decay matter but it is also the residence of fungi, nematodes, protozoa, insects and their products, as well as human-derived recalcitrant substances, all of them constitute an enormous array of potential food for most diverse microbes. Their use would benefit not only microbes but also their plant hosts when making nutrients available. Soil bacteria have major roles in nutrient cycles. Phosphorus solubilizing rhizospheric bacteria promote plant growth (Rodríguez and Fraga, 1999) and microorganisms participate in plant mineral acquisition (Hinsinger, 1998).

LIFE AT THE RHIZOSPHERE FROM A NUTRITIONAL PERSPECTIVE

Different rhizosphere bacteria may have preferences for distinct substrates (Shaw et al., 2006) and this would allow a complex community to be established at the rhizosphere. Different parts of the roots are colonized by different microbes and exudation and rhizodeposition varies qualitatively in different parts of the roots (Badri and Vivanco, 2009; Dennis et al., 2010). Some plants may exude more than others (Dennis et al., 2010) and maintain larger microbial populations. Results from a proteomic-based analysis suggested that bacteria may adapt to a new range of nutrients from exudates (Cordeiro et al., 2013).

We documented simultaneous assimilation of different substrates in *Rhizobium* (Romanov and Martínez-Romero, 1994; Romanov et al., 1994). This type of metabolism would be advantageous at the rhizosphere and it has been observed in rhizoremediation (González-Paredes et al., 2013). To nourish on several plant exudated substances at the same time as well as from diverse soil substances could be a characteristic of successful rhizospheric bacteria. Genes encoding enzymes for the utilization of some Amadori compounds that may be found in the rhizosphere are patchily distributed in rhizobia (Baek et al., 2005) indicating that not all bacteria have the same degrading capacities. We have compared rhizospheric bacteria to gut bacteria in the process of digesting and converting food to host usable products (Ramírez-Puebla et al., 2013).

Pseudomonas, *Burkholderia*, *Streptomyces*, and rhizobia have high degrading capabilities (Kontchou and Blondeau, 1992; Juhasz et al., 1996, 2003). All may be found associated to roots and their high degrading capacities may be advantageous in rhizospheres. They have also characteristic large genomes (for examples, Bentley et al., 2002; Kaneko et al., 2002; Paulsen et al., 2005; Yan et al., 2008; Ormeño-Orrillo et al., 2012) that may be in relation to their high degrading capabilities. We suggested that many rhizobial genes of unknown function participate in the catabolism of root, rhizospheric, and soil substances (Ormeño-Orrillo and Martínez-Romero, 2013) and this could apply to other soil and rhizospheric bacteria as well.

Interestingly mutants in single genes involved in nutrient usage at the rhizosphere (Rosenblueth et al., 1998; Ramachandran et al., 2011) normally do not have clear phenotypes indicating that there are other substrates available that may be used by bacteria at the rhizosphere.

In modern times, rhizospheric microorganisms are exposed as well to anthropogenic contaminants (González-Paredes et al., 2013). Rhizoremediation takes advantage of the degrading capabilities of rhizospheric microorganisms. Organic matter in soil strongly influences the fate of contaminants (Li et al., 2011).

CONCLUDING REMARKS

After considering the large diversity of potential nutrients (from rhizodeposits, root exudates, seeds, decaying organic matter, soil, and the rhizosphere community itself) for microbes at the rhizosphere we propose a hypothesis for bacterial nutrition at the rhizosphere: a buffet hypothesis where commensals choose their food from a diversity of options. This is in contrast to the proposal of oligotrophy at the rhizosphere (Ramachandran et al., 2011). Copiotrophic rhizobia are very successful rhizosphere colonizers (Gutiérrez-Zamora and Martínez-Romero, 2001). Microbial respiration is not carbon limited in the rhizosphere (Cheng et al., 1996). Rhizosphere is a complex environment with substitutable resources. In experimental evolution in complex environments with substitutable resources, *Pseudomonas* lineages evolved as imperfect generalists that differentiate to assimilate a certain range of substrates but not all (Barrett et al., 2005), this seems to happen with microbes at the rhizosphere.

ACKNOWLEDGMENTS

To PAPIIT IN205412 from UNAM. To M. Dunn for reading the manuscript. Martha G. López-Guerrero was a PhD student at the Programa de Doctorado en Ciencias Biomédicas, UNAM and had a fellowship from CONACyT, México. We apologize to authors who have contributed to the area and were not referred due to space limitations.

REFERENCES

Badri, D. V., Chaparro, J. M., Zhang, R., Shen, Q., and Vivanco, J. M. (2013). Application of natural blends of phytochemicals derived from the root exudates of *Arabidopsis* to the soil reveal that phenolic-related compounds predominantly modulate the soil microbiome. *J. Biol. Chem.* 288, 4502–4512. doi: 10.1074/jbc.M112.433300

Badri, D. V., and Vivanco, J. M. (2009). Regulation and function of root exudates. *Plant Cell Environ.* 32, 666–681. doi: 10.1111/j.1365-3040.2009.01926.x

Baek, C. H., Farrand, S. K., Lee, K. E., Park, D. K., Lee, J. K., and Kim, K. S. (2003). Convergent evolution of Amadori opine catabolic systems in plasmids of *Agrobacterium tumefaciens*. *J. Bacteriol.* 185, 513–524. doi: 10.1128/JB.185.2.513-524.2003

Baek, C. H., Farrand, S. K., Park, D. K., Lee, K. E., Hwang, W., and Kim, K. S. (2005). Genes for utilization of deoxyfructosyl glutamine (DFG), an amadori compound, are widely dispersed in the family Rhizobiaceae. *FEMS Microbiol. Ecol.* 53, 221–233. doi: 10.1016/j.femsec.2004.12.008

Baelum, J., Nicolaisen, M. H., Holben, W. E., Strobel, B. W., Sørensen, J., and Jacobsen, C. S. (2008). Direct analysis of *tfdA* gene expression by indigenous bacteria in phenoxy acid amended agricultural soil. *ISME J.* 2, 677–687. doi: 10.1038/ismej.2008.21

Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S., and Vivanco, J. M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu. Rev. Plant Biol.* 57, 233–266. doi: 10.1146/annurev.arplant.57.032905.105159

Barrett, R. D., MacLean, R. C., and Bell, G. (2005). Experimental evolution of *Pseudomonas fluorescens* in simple and complex environments. *Am. Nat.* 166, 470–480. doi: 10.1086/444440

Bauer, W. D., and Robinson, J. B. (2002). Disruption of bacterial quorum sensing by other organisms. *Curr. Opin. Biotechnol.* 13, 234–237. doi: 10.1016/S0958-1669(02)00310-5

Bentley, S. D., Chater, K. F., Cerdeño-Tárraga, A. M., Challis, G. L., Thomson, N. R., James, K. D., et al. (2002). Complete genome sequence of the model actinomycete *Streptomyces coelicolor* A3(2). *Nature* 417, 141–147. doi: 10.1038/417141a

Berendsen, R. L., Pieterse, C. M., and Bakker, P. A. (2012). The rhizosphere microbiome and plant health. *Trends Plant Sci.* 17, 478–486. doi: 10.1016/j.tplants.2012.04.001

Brown, S. A., Palmer, K. L., and Whiteley, M. (2008). Revisiting the host as a growth medium. *Nat. Rev. Microbiol.* 6, 657–666. doi: 10.1038/nrmicro1955

Bulgarelli, D., Rott, M., Schlaeppi, K., Ver Loren van Themaat, E., Ahmadinejad, N., Assenza, F., et al. (2012). Revealing structure and assembly cues for *Arabidopsis* root-inhabiting bacterial microbiota. *Nature* 488, 91–95. doi: 10.1038/nature11336

Cheng, W., Zhang, Q., Coleman, D. C., Carroll, C. R., and Hoffman, C. A. (1996). Is available carbon limiting microbial respiration in the rhizosphere? *Soil Biol. Biochem.* 28, 1283–1288. doi: 10.1016/S0038-0717(96)00138-1

Cordeiro, F. A., Tadra-Sfeir, M. Z., Huergo, L. F., de Oliveira Pedrosa, F., Monteiro, R. A., and de Souza, E. M. (2013). Proteomic analysis of *Herbaspirillum seropedicae* cultivated in the presence of sugar cane extract. *J. Proteome Res.* 12, 1142–1150. doi: 10.1021/pr300746j

de Bruijn, F. J. (eds). (2013). *Molecular Microbial Ecology of The Rhizosphere.* Hoboken, NJ: Wiley-Blackwell Publishers.

Dennis, P. G., Miller, A. J., and Hirsch, P. R. (2010). Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? *FEMS Microbiol. Ecol.* 72, 313–327. doi: 10.1111/j.1574-6941.2010.00860.x

Ferrer, J. L., Austin, M. B., and Stewart, C. Jr., Noel, J. P. (2008). Structure and function of enzymes involved in the biosynthesis of phenylpropanoids. *Plant Physiol. Biochem.* 46, 356–370. doi: 10.1016/j.plaphy.2007.12.009

Fincher, G. B., Stone, B. A., and Clarke, A. E. (1983). Arabinogalactan-proteins: structure, biosynthesis and function. *Annu. Rev. Plant Physiol.* 34, 47–70. doi: 10.1146/annurev.pp.34.060183.000403

Fischer, D., Pfitzner, B., Schmid, M., Simões-Araújo, J. L., Reis, V. M., Pereira, W., et al. (2012). Molecular characterisation of the diazotrophic bacterial community in uninoculated and inoculated field-grown sugarcane (*Saccharum* sp.). *Plant Soil* 356, 83–99. doi: 10.1007/s11104-011-0812-0

Flores, H. E., Vivanco, J. M., and Loyola-Vargas, V. M. (1999). 'Radicle' biochemistry: the biology of root-specific metabolism. *Trends Plant Sci.* 4, 220–226. doi: 10.1016/S1360-1385(99)01411-9

Friesen, M. L., Porter, S. S., Stark, S. C., von Wettberg, E. J., Sachs, J. L., and Martinez-Romero, E. (2011). Microbially mediated plant functional traits. *Annu. Rev. Ecol. Evol. Syst.* 42, 23–46. doi: 10.1146/annurev-ecolsys-102710-145039

González-Paredes, Y., Alarcón, A., Ferrera-Cerrato, R., Almaraz, J. J., Martínez-Romero, E., Cruz-Sánchez, J. S., et al. (2013). Tolerance, growth and degradation of phenanthrene and benzo[a]pyrene by *Rhizobium tropici* CIAT 899 in liquid culture medium. *Appl. Soil Ecol.* 63, 105–111. doi: 10.1016/j.apsoil.2012.09.010

González-Pasayo, R., and Martínez-Romero, E. (2000). Multiresistance genes of *Rhizobium etli* CFN42. *Mol. Plant Microbe Interact.* 13, 572–577. doi: 10.1094/MPMI.2000.13.5.572

Gutiérrez-Zamora, M. L., and Martínez-Romero, E. (2001). Natural endophytic association between *Rhizobium etli* and maize (*Zea mays* L.). *J. Biotechnol.* 91, 117–126. doi: 10.1016/S0168-1656(01)00332-7

Haichar, F. Z., Marol, C., Berge, O., Rangel-Castro, J. I., Prosser, J. I., Balesdent, J., et al. (2008). Plant host habitat and root exudates shape soil bacterial community structure. *ISME J.* 2, 1221–1230. doi: 10.1038/ismej.2008.80

Hassan, S., and Mathesius, U. (2012). The role of flavonoids in root-rhizosphere signalling: opportunities and challenges for improving plant–microbe interactions. *J. Exp. Bot.* 63, 3429–3444. doi: 10.1093/jxb/err430

Hiltner, L. (1904). Über neuere Erfahrungen und Probleme auf dem Gebiete der Bodenbakteriologie unter besonderer Berücksichtigung der Gründüngung und Brache. *Arb. Dtsch. Landwirtsch. Gesellschaft* 98, 59–78.

Hinsinger, P. (1998). How do plant roots acquire mineral nutrients? Chemical processes involved in the rhizosphere. *Adv. Agron.* 64, 225–265. doi: 10.1016/S0065-2113(08)60506-4

Hirsch, P. R., and Mauchline, T. H. (2012). Who's who in the plant root microbiome? *Nat. Biotechnol.* 30, 961–962. doi: 10.1038/nbt.2387

Juhasz, A. L., Britz, M. L., and Stanley, G. A. (1996). Degradation of high molecular weight polycyclic aromatic hydrocarbons by *Pseudomonas cepacia*. *Biotechnol. Lett.* 18, 577–582. doi: 10.1007/BF00140206

Juhasz, A. L., Britz, M. L., and Stanley, G. A. (2003). Degradation of fluoranthene, pyrene, benz[a]anthracene and dibenz[a,h]anthracene by *Burkholderia cepacia*. *J. Appl. Microbiol.* 83, 189–198. doi: 10.1046/j.1365-2672.1997.00220.x

Kaneko, T., Nakamura, Y., Sato, S., Minamisawa, K., Uchiumi, T., Sasamoto, S., et al. (2002). Complete genomic sequence of nitrogen-fixing symbiotic bacterium *Bradyrhizobium japonicum* USDA110. *DNA Res.* 9, 189–197. doi: 10.1093/dnares/9.6.189

Kontchou, C. Y., and Blondeau, R. (1992). Biodegradation of soil humic acids by *Streptomyces viridosporus*. *Can. J. Microbiol.* 38, 203–208. doi: 10.1139/m92-034

Li, C., Berns, A. E., Schäffer, A., Séquaris, J. M., Vereecken, H., Ji, R., et al. (2011). Effect of structural composition of humic acids on the sorption of a branched nonylphenol isomer. *Chemosphere* 84, 409–414. doi: 10.1016/j.chemosphere.2011.03.057

López-Guerrero, M. G., Ormeño-Orrillo, E., Acosta, J. L., Mendoza-Vargas, A., Rogel, M. A., Ramírez, M. A., et al. (2012). Rhizobial extrachromosomal replicon variability, stability and expression in natural niches. *Plasmid* 68, 149–158. doi: 10.1016/j.plasmid.2012.07.002

Lott, J. N. A., Ockenden, I., Raboy, V., and Batten, G. D. (2000). Phytic acid and phosphorus in crop seeds and fruits: a global estimate. *Seed Sci. Res.* 10, 11–33.

Lundberg, D. S., Lebeis, S. L., Paredes, S. H., Yourstone, S., Gehring, J., Malfatti, S., et al. (2012). Defining the core *Arabidopsis thaliana* root microbiome. *Nature* 488, 86–90. doi: 10.1038/nature11237

Majewska-Sawka, A., and Nothnagel, E. A. (2000). The multiple roles of arabinogalactan proteins in plant development. *Plant Physiol.* 122, 3–10. doi: 10.1104/pp.122.1.3

Mathesius, U., and Watt, M. (2011). "Rhizosphere signals for plant–microbe interactions: implications for field-grown plants," in *Progress in Botany*, Vol. 72, eds U. Lüttge, W. Beyschlag, B. Büdel, and D. Francis (Berlin: Springer-Verlag), 125–161.

Nebbioso, A., and Piccolo, A. (2001). Basis of a humeomics science: chemical fractionation and molecular characterization of humic biosuprastructures. *Biomacromolecules* 12, 1187–1199. doi: 10.1021/bm101488e

Ormeño-Orrillo, E., and Martínez-Romero, E. (2013). Phenotypic tests in *Rhizobium* species description: an opinion and (a sympatric speciation) hypothesis. *Syst. Appl. Microbiol.* 36, 145–147. doi: 10.1016/j.syapm.2012.11.009.

Ormeño-Orrillo, E., Rogel, M. A., Chueire, L. M., Tiedje, J. M., Martínez-Romero, E., and Hungria, M. (2012). Genome sequences of *Burkholderia* sp. strains CCGE1002 and H160, isolated from legume nodules in Mexico and Brazil. *J. Bacteriol.* 194, 6927. doi: 10.1128/JB.01756-12

Paulsen, I. T., Press, C. M., Ravel, J., Kobayashi, D. Y., Myers, G. S., Mavrodi, D. V., et al. (2005). Complete genome sequence of the plant commensal *Pseudomonas fluorescens* Pf-5. *Nat. Biotechnol.* 23, 873–878. doi: 10.1038/nbt1110

Phillips, D. A., Joseph, C. M., Yang, G. P., Martinez-Romero, E., Sanborn, J. R., and Volpin, H. (1999). Identification of lumichrome as a *Sinorhizobium* enhancer of alfalfa root respiration and shoot growth. *Proc. Natl. Acad. Sci. U.S.A.* 96, 12275–12280. doi: 10.1073/pnas.96.22.12275

Ramachandran, V. K., East, A. K., Karunakaran, R., Downie, J. A., and Poole, P. S. (2011). Adaptation of *Rhizobium leguminosarum* to pea, alfalfa and sugar beet rhizospheres investigated by comparative transcriptomics. *Genome Biol.* 12, R106. doi: 10.1186/gb-2011-12-10-r106

Ramírez-Puebla, S. T., Servín-Garcidueñas, L. E., Jiménez-Marín, B., Bolaños, L. M., Rosenblueth, M., Martínez, J., et al. (2013). Gut and root microbiota commonalities. *Appl. Environ. Microbiol.* 79, 2–9. doi: 10.1128/AEM.02553-12

Rodríguez, H., and Fraga, R. (1999). Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnol. Adv.* 17, 319–339. doi: 10.1016/S0734-9750(99)00014-2

Romanov, V. I., Hernández-Lucas, I., and Martínez-Romero, E. (1994). Carbon metabolism enzymes of *Rhizobium tropici* cultures and bacteroids. *Appl. Environ. Microbiol.* 60, 2339–2342. doi: 10.1007/s11104-007-9481-4

Romanov, V. I., and Martínez-Romero, E. (1994). Sucrose transport and hydrolysis in *Rhizobium tropici. Plant Soil* 161, 91–96. doi: 10.1007/BF02183088

Rosenblueth, M., Hynes, M. F., and Martínez-Romero, E. (1998). *Rhizobium tropici teu* genes involved in specific uptake of *Phaseolus vulgaris* bean-exudate compounds. *Mol. Gen. Genet.* 258, 587–598. doi: 10.1007/s004380050772

Rosenblueth, M., and Martínez-Romero, E. (2006). Bacterial endophytes and their interactions with hosts. *Mol. Plant Microbe Interact.* 19, 827–837. doi: 10.1094/MPMI-19-0827

Scheffknecht, S., Mammerler, R., Steinkellner, S., and Vierheilig, H. (2006). Root exudates of mycorrhizal tomato plants exhibit a different effect on microconidia germination of *Fusarium oxysporum* f. sp. *lycopersici* than root exudates from non-mycorrhizal tomato plants. *Mycorrhiza* 16, 365–370. doi: 10.1007/s00572-006-0048-7

Shaw, L. J., Morris, P., and Hooker, J. E. (2006). Perception and modification of plant flavonoid signals by rhizosphere microorganisms. *Environ. Microbiol.* 8, 1867–1880. doi: 10.1111/j.1462-2920.2006.01141.x

Snoeck, C., Verreth, C., Hernández-Lucas, I., Martínez-Romero, E., and Vanderleyden, J. (2003). Identification of a third sulfate activation system in *Sinorhizobium* sp. strain BR816: the CysDN sulfate activation complex. *Appl. Environ. Microbiol.* 69, 2006–2014. doi: 10.1128/AEM.69.4.2006-2014.2003

van Loon, L. C., Bakker, P. A., and Pieterse, C. M. (1998). Systemic resistance induced by rhizosphere bacteria. *Annu. Rev. Phytopathol.* 36, 453–483. doi: 10.1146/annurev.phyto.36.1.453

Walker, T. S., Bais, H. P., Grotewold, E., and Vivanco, J. M. (2003). Root exudation and rhizosphere biology. *Plant Physiol.* 132, 44–51. doi: 10.1104/pp.102.019661

Yan, Y., Yang, J., Dou, Y., Chen, M., Ping, S., Peng, J., et al. (2008). Nitrogen fixation island and rhizosphere competence traits in the genome of root-associated *Pseudomonas stutzeri* A1501. *Proc. Natl. Acad. Sci. U.S.A.* 105, 7564–7569. doi: 10.1073/pnas.0801093105

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 13 March 2013; accepted: 23 May 2013; published online: 14 June 2013.

Citation: López-Guerrero MG, Ormeño-Orrillo E, Rosenblueth M, Martinez-Romero J and Martínez-Romero E (2013) Buffet hypothesis for microbial nutrition at the rhizosphere. Front. Plant Sci. ***4****:188. doi: 10.3389/fpls.2013.00188*

This article was submitted to Frontiers in Functional Plant Ecology, a specialty of Frontiers in Plant Science.