Buffet hypothesis for microbial nutrition at the rhizosphere

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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 (Rosenbluth 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 Hilzner (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, 107 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 (Barlum 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 Nöthig, 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; Bremersden et al., 2012) as prebiotics do (Ramírez-Puebla et al., 2013) and additionally, just adhesion to plant lignocellulose acts to select bacteria from the soil (Bulgarelli et al.,...
Additionally, plant-derived substances may control bacterial growth (Scheffknecht et al., 2006). Plants may control bacterial growth with antimicrobials such as phytoalexins (González-Pasayo and Martínez-Romero, 2006; Shaw et al., 2006), bacterial-quorum plant-produced mimics (Bauer and Robinson, 2005), or by inducing changes in plant production of exudates (Lott et al., 2000). Germinated seedlings provide enough sulfur in root exudates for bacterial growth (Snoeck et al., 2003).

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choose their food from a diversity of options. This is in contrast to the proposal of oligotrophy at the rhizosphere (Ramachandran et al., 2011). Caprotrophic rhizobia are very successful rhizosphere colonizers (Cátedra-Zamora and Martinez-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

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