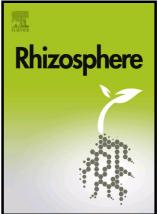
## Author's Accepted Manuscript

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## ACCEPTED MANUSCRIPT

Managing and manipulating the rhizosphere microbiome for plant health: A systems approach

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Abstract

Plants co-evolved with microbes, and plant genotypes that supported microbiomes that increased their own health likely had a fitness advantage under natural selection. Plant domestication and crop breeding under fertilization have largely decoupled the rhizosphere microbiome from plant selection. If important interactions have been lost as a result, there is an exciting opportunity to re-engineer characteristics of beneficial rhizosphere microbiomes back into agricultural cropping systems. New tools will allow us to engineer the rhizosphere with increasing sophistication in the future, but must recognize that the rhizosphere is a highly connected and interactive system.

Plant-microbe rhizosphere interactions: Evolution of the holobiont

Plants evolved into a microbial world. When the earliest plants extended their roots into primordial soil, they encountered a habitat already teeming with bacterial and fungal life (Heckman et al. 2001). From day one, plants likely started to influence the rhizosphere microbiome. Their roots altered the physical structure of soils. They extracted nutrients from the soil, competing with microbes. They extracted water from the soil, altering the soil moisture regime encountered by microbes. Their detritus led to the accumulation of organic carbon which was then processed by heterotrophic microbes, leading to the formation of soil organic matter (SOM) (Cotrufo et al. 2013, Lehmann and Kleber 2015). As they began leaking carbon-rich substrates through their roots, those labile substrates likely favored microbes that could quickly assimilate them (Doornbos et al. 2012). By altering the physical and chemical environment in the rhizosphere, plants affected the fitness of different microbial groups, interactions among microbes, and spurred evolution of new microbes better suited to life in the rhizosphere (Lambers et al. 2009).

There is now overwhelming evidence that plants engineer the rhizosphere microbiome (Chaparro et al. 2014). Even the most ancient lineages of plants show a strong ability to alter the relative abundance of microbial groups in the soils surrounding the rhizosphere (Valverde et al. 2016). Different plant species support unique microbiomes (Gertsson and Alsanius 2001). These contrasting microbiomes have been attributed to differences in root exudate chemistry (Bais et al. 2006, Rasmann and Turlings 2016) and in plant nutrient uptake rates (Bell et al. 2015).

Given that plants can affect the rhizosphere microbiome through numerous mechanisms and that the microbiome can affect plant health (Berendsen et al. 2012, Mueller and Sachs 2015), a reasonable hypothesis emerges: Genotypic and phenotypic variations in plant traits that support microbiomes that increase plant nutrient availability, prevent pathogens or otherwise enhance plant health, growth and performance incur a fitness advantage. Thus, *the ability of a plant to support a beneficial microbiome is a plant trait under selection*. The fitness advantage incurred by the microbiome must outweigh the cost to the plant in diverted C and energy. The close symbiosis of plants and microbes can be viewed as an

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