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## Understanding plant-microorganism interactions to envision a future of sustainable agriculture

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Interactions between microorganisms and plants are multifaceted and involve a network of integrated physiological responses, chemical cross-talk and regulatory circuits interconnecting both associates. These interactions are the result of co-evolution that began with the appearance of plants 700 million years ago. The immense extent of this co-evolution explains the complexity and specificity of these interactions, which can be classified into four main types: symbiosis, mutualism, commensalism and pathogenesis. Understanding the mechanistic basis of these relations and the physiological aspects that induce them is key to building effective strategies for sustainable agriculture. Broadly speaking, biological solutions embrace two crucial aspects of sustainable agriculture: the use of living non-hazardous organisms or their derivatives to directly increase crop yields – known as biostimulants – or to protect them from pests and diseases – known as biocontrol agents –. To tell a successful story on biological solutions, there is a pressing need to integrate different perspectives from diverse research fields with the widest vision to the most specific *i.e.* from the ecology of natural and agricultural ecosystems to the biochemistry of important molecules and through the development of populations and the molecular biology of individuals. This exercise of integration of fields and perspectives is crucial to progress in a research sector that is becoming increasingly important and socially relevant. The position of the majority of national and European governments in this matter is also clear. Agriculture has to meet the needs of a constantly growing population, but this cannot come at an increased cost for the environment: future agricultural growth must be sustainable. Accordingly, measures including chemical pesticides or fertilizers that contaminate soil and underground water or that are a threat to animal or human health are being banned or are under surveillance, increasing the urgency to identify environmentally friendly alternatives. Although the benefits of using biological solutions to increase yield and protect crops from pests and diseases are undoubted, the sustainable-agricultural biotechnology industry encounters some common problems historically found in the pharmaceutical industry: a long, tedious and expensive process between the identification of a new product (living microorganism or derivative) and the entry to the market. This bottleneck can be overcome by substantially increasing both

available funding, and the number of researchers tackling the basic science that will enable the development of effective biological applications. Some of the most important and promising research lines approaching such solutions from different angles are described below.

Positive interactions between microorganisms and crops (e.g. symbiosis and mutualism) facilitate important processes, including biological fixation of nitrogen or solubilisation and mineralization of inorganic and organic phosphorous respectively, which can reduce the use of chemical fertilizers (Pérez-Montaño *et al.*, 2014). On the other hand, understanding the molecular basis of microorganisms' pathogenicity towards plants will enable the development of strategies to block the causal agents – known as phytopathogens – of plant diseases (Leonard *et al.*, 2017). Indirectly, biocontrol agents with the capacity to outcompete phytopathogens are excellent candidates to prevent infections and sequentially increase crop productivity, not only in the field but also to avoid post-harvest losses (Leneveu-Jenvrin *et al.*, 2019). Importantly, some biocontrol agents present additional positive features such as the capacity to trigger systemic resistance in plants, another exceptional mechanism of infection prevention (Pieterse *et al.*, 2014). An important characteristic that enables biocontrol agents to carry out their functions is the formation of biofilms on plant surfaces (roots, leaves and seeds). This is an important step in plant colonization and in some cases, the microbial biofilm formed on crops surfaces protects the plant (Pandin *et al.*, 2017). Secretion systems are also well known for playing an essential role in plant-microbe interactions, particularly the type III and type VI secretion systems (T3SS and T6SS). The T3SS is widespread in plant pathogens and responsible for virulence, broadly defined as the degree of damage caused to the host. The T6SS is found in both beneficial bacteria and phytopathogens and it is mainly involved in inter-bacterial competition being recently identified as a powerful mechanism of biocontrol (Bernal *et al.*, 2017). Interestingly, The T3SS has an alternative beneficial role in the symbioses of rhizobia with their host plants (Marie *et al.*, 2001) while the studies defining the role of the T6SS in rhizobia species are still at an early stage (Salinero-Lanzarote *et al.*, 2019).

A flourishing field with promising implications in sustainable agriculture is that of the membrane vesicles as vehicles to transport molecules of interest that could block virulence factors, enhance the plant immune system or eliminate surrounding phytopathogens (Borrero de Acuña and Bernal, 2021).

In this special issue of *Environmental Microbiology* “Multifaceted Plant-Microbe Interactions”, we have brought together thirty-four research articles, a minireview and an Opinion article covering this relevant theme. An important method article describes a bioluminescence-fluorescence approach to monitoring bacterial localization. This work is extremely useful for the study and characterization of the plant holobiont. Twelve articles cover different aspects of research into beneficial microbes including five on the importance of fungi. Research articles focusing on beneficial fungi include studies of species of *Serendipita* and *Pisolithus* and also the characterization of fungal volatile compounds, all with the capacity of promoting growth in a variety of plants such as wheat, eucalyptus, agaves and cacti. Well-known plant growth-promoting rhizobacteria (PGPR) are also represented with studies of *Pseudomonas* and *Bacillus* as the archetypal genera of gram-negative and gram-positive plant-beneficial bacteria. A study identifies a novel transcriptional regulator (EmhR) of *P. fluorescens* controlling the signalling molecule indole, which enhanced antibiotic resistance in this microorganism. Another study describes the role of the extracellular matrix of *P. chlororaphis* in the formation of biofilm and the contribution to the biological control activity of this important biocontrol agent in avocado plants. Genes encoding the proteins responsible for *B. thuringiensis* lysine metabolism and thus the synthesis of insecticidal crystal proteins are characterized in another article, providing new strategies for the construction of more potent insecticidal strains. Three articles focus on the rhizobium-leguminous symbiosis that enables nitrogen fixation by the bacterium for the benefit of the plant. These include the analysis of pathways involved in root colonization and symbiosis in *Rhizobium radiobacter* and nitrate reduction in *Bradyrhizobium* isolates. An opinion article revolves around the idea of symbionts being specific to their hosts to gain efficacy and the possibility that reverting this (*i.e.* being

less specific) would lead to a broadening of the microbial host-range, a desirable characteristic from an agricultural point of view. Finally, one minireview highlights the plant endosphere, describing bacterial life within plants.

Nine articles are focused on pathogenic fungi, including *Botrytis*, *Epichloe*, *Verticillium* and *Fusarium* species describing important effectors (Av2, VdBre1, AvrFom2), novel antagonistic bacteria such as *Streptomyces pratensis* and a new family of genes key for fungal adaptation to their niches. A further research article describes the colonization dynamics of the bacterial phytopathogen *Pantoea agglomerans* in the wheat root.

Last but not least, we delve into the importance of plant microbiota. Understanding the composition and dynamics of the plant holobiont is instrumental to prevent pest predation and infection and thus to maintain healthy crops with profitable yields. Representing the importance of this fast-moving field on environmental microbiology, a significant number of research articles (fifteen) are dedicated to plant microbiomes and mycobiomes in different hosts and ecosystems such as grapevine, oak, mulberry tree, seagrass, fern, sugarcane silage, alpine permafrost, boreal peatland forests and even plant-related insects such as aphids.

We hope this collection of research articles, opinion and minireviews is enjoyable and enlightening for the interested Environmental Microbiology readers.

Bernal, P., Allsopp, L.P., Filloux, A., and Llamas, M.A. (2017) The *Pseudomonas putida* T6SS is a plant warden against phytopathogens. *The ISME Journal* **11**: 972–987.

Borrero-de -Acuña, J.M. and Bernal, P. (2021) Plant holobiont interactions mediated by the type VI secretion system and the membrane vesicles: promising tools for a greener agriculture. *Environ Microbiol.*

Leneuve-Jenvrin, C., Charles, F., Barba, F.J., and Remize, F. (2019) Role of biological control agents and physical treatments in maintaining the quality of fresh and minimally-processed fruit and vegetables. *Crit Rev Food Sci* **60**: 1–19.

Leonard, S., Hommais, F., Nasser, W., and Reverchon, S. (2017) Plant–phytopathogen interactions: bacterial responses to environmental and plant stimuli. *Environ Microbiol* **19**: 1689–1716.

Marie, C., Broughton, W.J., and Deakin, W.J. (2001) Rhizobium type III secretion systems: legume charmers or alarmers? *Curr Opin Plant Biol* **4**: 336–342.

Pandin, C., Coq, D.L., Canette, A., Aymerich, S., and Briandet, R. (2017) Should the biofilm mode of life be taken into consideration for microbial biocontrol agents? *Microb Biotechnol* **10**: 719–734.

Pérez-Montaño, F., Alías-Villegas, C., Bellogín, R.A., Cerro, P. del, Espuny, M.R., Jiménez-Guerrero, I., et al. (2014) Plant growth promotion in cereal and leguminous agricultural important plants: From microorganism capacities to crop production. *Microbiol Res* **169**: 325–336.

Pieterse, C.M.J., Zamioudis, C., Berendsen, R.L., Weller, D.M., Wees, S.C.M. van, and Bakker, P.A.H.M. (2014) Induced Systemic Resistance by Beneficial Microbes. *Annu Rev Phytopathol* **52**: 1–29.

Salinero-Lanzarote, A., Pacheco-Moreno, A., Domingo-Serrano, L., Durán, D., Ormeño-Orrillo, E., Martínez-Romero, E., et al. (2019) The Type VI secretion system of *Rhizobium etli* Mim1 has a positive effect in symbiosis. *Fems Microbiol Ecol* **95**..

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