

SOIL-BORNE LEGACIES OF PLANT DISEASE

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THE ROOT MICROBIOME

There is a mesmerizing number and diversity of microbes associated with plants, especially in and around the roots. Collectively the microbes associated with the plant root form the root microbiome and its composition largely determines plant health (Berendsen et al., 2012). Although some pathogenic microbes are very harmful to plants, most members of the root microbiome do not cause disease in plants and some of these microbes even protect and promote plant growth (Glick et al., 2007; Berendsen et al., 2012; Philippot et al., 2013; Bakker et al., 2018). Plants shape the composition of root

microbiome by secreting mixtures of microbe-stimulatory or impeding chemicals (Badri and Vivanco, 2009; Sasse et al., 2018; Zhalnina et al., 2018). Genetic differences between plants determine the composition of root exudates and the dynamics by which they are produced. Root microbiomes can consequently differ substantially between plant species and even between genotypes within a species (Lundberg et al., 2012; Edwards et al., 2015). This implies that plant genetics can contribute to the selection of a protective plant microbiome.

DISEASE-SUPPRESSIVE SOILS

The protective effect of root-associated microbial communities is best evidenced by disease-suppressive soils, in which susceptible host plants do not develop disease despite the presence of a virulent pathogen (Schlatter et al., 2017). Disease-suppressive soils have been identified for different plant species and plant pathogens. In most cases, the disease suppression is related to the presence of one, or a few, microbial species that can antagonize the pathogen either directly or indirectly by priming the plant's immune system. Arguably, the best-studied disease-suppressive soils are soils that have become suppressive to take-all disease of

wheat (Weller et al., 2002; Schlatter et al., 2017). Take-all suppressive soils have been found around the world and similar antifungal-producing *Pseudomonads* have been connected to disease suppressiveness in different fields. This implies that these specific microbes are present in all of these fields and the plant is able to select and enrich these specific bacteria from the enormous diversity of microbes that each soil comprises. It implies not only a very strict and long co-evolution of the plant with certain beneficial microbes, but also that these microbes are ubiquitously present. Take-all suppressive soils typically develop after a major disease

outbreak, implying that upon attack plants cry out for help and recruit specific microbes to come to their aid.

CRY FOR HELP

Recently, we tested this ‘cry for help’ hypothesis and found that, when leaves of the model plant species *Arabidopsis thaliana* (hereafter referred to as *Arabidopsis*) were inoculated with the downy-mildew pathogen *Hyaloperonospora arabidopsidis* (Hpa), a subsequent population of plants growing in the soil conditioned by the infected plants was more resistant to this pathogen (Berendsen et al., 2018). Moreover, foliar infection by this pathogen resulted in the specific promotion of a consortium of three bacterial species on the *Arabidopsis* roots. These bacterial strains became highly abundant in the rhizosphere of Hpa-infected *Arabidopsis* plants, and were isolated. Upon application to soil, these bacteria separately did not significantly affect plant performance. However, when applied together, this consortium of three

strains protected *Arabidopsis* against Hpa infection and it promoted plant growth. Similarly, infections of *Arabidopsis* by the bacterial leaf pathogen *Pseudomonas syringae* gave rise to a root microbiome that could protect subsequent populations of plants against this pathogen (Yuan et al., 2018). Also in pepper and wheat plants, defence activation and subsequent systemic signalling led to changes in the root microbiome that were suggested to benefit the plant (Dudenhöffer et al., 2016; Kong et al., 2016). Together, these studies illustrate that plants can rapidly adjust their root microbiome in response to disease and recruit disease suppressing microbes, giving rise to a ‘soil-borne legacy’ that protects the next generation of plants growing in the same soil (Bakker et al., 2018).

INDUCED SYSTEMIC RESISTANCE

It is known that colonization of *Arabidopsis* roots by specific microbes can trigger induced systemic resistance (ISR) (Pieterse et al., 1996; van Wees et al., 1997). Using the ISR-model strain *Pseudomonas simiae* WCS417, the root-specific transcription factor MYB72 was identified as an essential regulator of ISR (van der Ent et al., 2008). MYB72 is rapidly activated upon root colonization by diverse ISR-inducing microbes and controls a large gene-regulatory network that is required for the establishment of ISR in foliar tissues. Transcriptional analyses of mutant and overexpressing genotypes revealed that MYB72 upregulates

genes in the roots involved in the phenylpropanoid pathway (Zamioudis et al., 2014). The final products of this pathway are coumarins, phenolic compounds that have known antimicrobial effects. Recently, it was discovered that MYB72 indeed controls the biosynthesis and secretion of numerous compounds, including coumarins. Moreover, the rhizosphere microbiome composition of *Arabidopsis* wild-type plant is very different from mutant plants that are strongly impaired in coumarin production and secretion (Stringlis et al., 2018). This implies that MYB72 has a dual role in ISR, where it not only functions in

generating the systemic ISR signal, but may also play a critical role in shaping a root microbiome that elicits ISR. Preliminary results indicate that MYB72 is also required for the creation of a soilborne legacy of *Hpa*-infection

(Gilles Vismans, unpublished results). This highlights the role of this transcription factor as a key regulator of the plant's communication with its microbiome.

PERSPECTIVE

Plants are able to manage the composition of their root microbiomes in response to attack in a way that benefits the survival of their offspring. In nature, the build-up of specialized pathogen inoculum is thought to cause negative soil feedback that most strongly affects the performance of dominant plant species and changes the demography of wild plants (*Klironomos*, 2002; *Mommer* et al., 2018). In agriculture, pathogen build-up causes reduced yields in soils that have not

developed disease suppressiveness (*Cesarano* et al., 2017) and this is why most annual crops are planted in rotation. A 'cry for help' to the root microbiome could prove to be an integral part by which the plant immune system counteracts negative soil feedback. A fundamental understanding of these mechanisms could open up new ways to breed or engineer crop plants that are better able to create beneficial microbiomes and improve agricultural yields in a sustainable manner.

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