Soil-borne, a ferritale from the underground

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After 36 years in the Plant-Microbe Interactions (previously Phytopathology) group at Utrecht University, I retired from being soil-borne. It was heartwarming that the PMI group together with the KNPV working group Phytobacteriology, organized a symposium entitled "From PGPR to Plant Microbiome" to commemorate my retirement. The speakers at the symposium are all good friends who I met during different stages of my career. In 1984 my ferritale began in the group of Bob Schippers. In 1985 Philippe Lemanceau and David Weller were among the first International researchers who entered my life and never left. Not much later, in 1989, I had the great pleasure to work with Jos Raaijmakers for four years on his PhD project, and ever since our friendship continues. Almost twenty years later, in 2006, Roeland Berendsen entered my life and he is there to continue the soil-borne saga.

As mentioned by the first speaker Philippe Lemanceau in his lecture entitled "What amazing times we have been through!", the symposium "Iron, Siderophores, and Plant Diseases", that was organized in 1985 by Terry Swinburne and Bob Schippers (Swinburne, 1986), was an exciting starting point for a large group of scientists with an interest in Plant Growth Promoting Rhizobacteria (PGPR). Together with Claude Alabouvette, Philippe aimed to unravel the nature of disease suppressiveness in a Fusarium wilt suppressive soil and they discovered that microbial competition for both carbon and iron plays a prominent role (Lemanceau et al., 1988, 1992). The ferritale continued in Philippe's group, extending it to Fe uptake by Arabidopsis as influenced by siderophores (Vansuyt et al., 2017). The last decades Philippe's work shifted from PGPR to soil and plant microbiomes (Lemanceau et al., 2017), and more recently from plant microbiome to crop microbiome (Pivato et al., 2021).

"Iron man 4" was the provisional title of the lecture by Jos Raaijmakers, in which he pursued my secret lives as evidenced by the existence of the so-called soil-borne saga. The soil-borne sequels that refer to comments and opinions on current plant microbiome studies were actually started by Corné Pieterse in 2016 when he launched "The soil-borne supremacy" (Pieterse et al., 2016). This was then proceeded by "The soil-borne legacy" in 2018 (Bakker et al., 2018), "The soil-borne identity" in 2020 (Bakker et al., 2020), and "The soil-borne ultimatum" in 2022 (Bakker and Berendsen, 2022). To finalize the sequels, "soil-borne" was kept as a title for my retirement lecture. Hopefully this is the correct interpretation of the lecture by Jos. I must say it was a pity that he did not unveil at least some details about the latest breath-taking research from his group (Oyserman et al., 2022), in which concrete steps towards developing breeding programs for plant microbiomes are explored.

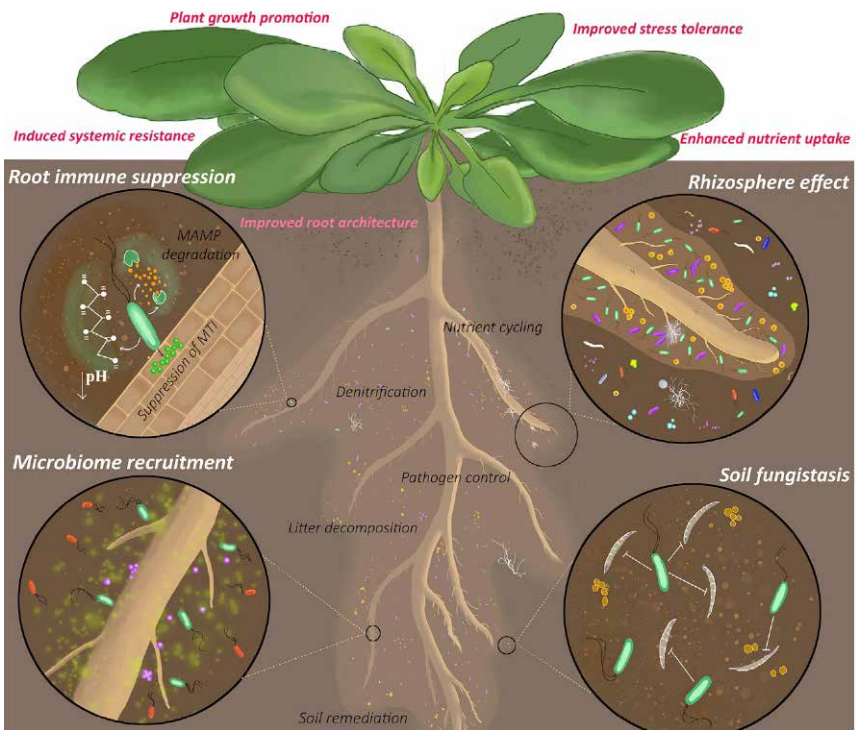
Next in line was Roeland Berendsen with a lecture entitled "the soil-borne legacy". Roeland shared details on how aboveground infection of Arabidopsis with *Hyaloperonospora arabidopsidis* leads to changes in the rhizosphere microbiome. Moreover, it results in protection against the pathogen in a next generation of Arabidopsis plants grown in the soil that was conditioned by *H. arabidopsidis* infected plants (Berendsen et al., 2018). This phenomenon of recruitment of a microbiome that can protect against disease was dubbed "the soil-borne legacy" (Bakker et al., 2018), and the legacy is not restricted to disease induced stress, but was also reported for shortage of the essential plant nutrient iron (Harbort et al., 2020), and for drought stress (Santos-Medellin, 2021). One of the final frontiers in plant microbiome research to which Roeland and his team significantly contribute, is to integrate basic knowledge in applications in sustainable agriculture, including development of elite microbiome composition and functioning from both microbiological and plant breeding perspectives.

Agricultural practices and farmers have always been the starting point for research in the group of David Weller. In his lecture entitled "PGPR and the Microbiome of Dryland and Irrigated Wheat" David took us to the wheat fields in Washington State and showed that some areas in which wheat is grown are so dry that farmers leave their field fallow for a year to save the precipitation to grow a crop the year after. Comparison of wheat-fallow-wheat and continuous wheat under irrigation reveals that different soil-borne pathogens develop under dry and irrigated conditions. In addition, under irrigated conditions the wheat rhizosphere microbiome is enriched with Pseudomonas spp. that produce the antibiotic 2,4-diacetylphloroglucinol, whereas under dry conditions Pseudomonas spp. that produce the antibiotic phenazine-1-carboxylic acid are enriched (Mavrodi et al., 2012a,b). Also in this work the ferritale was continued by the discovery that phenazine-1-carboxylic acid mobilizes iron in the rhizosphere of wheat (LeToureau et al., 2019).

My career has evolved around root colonizing Pseudomonas bacteria that produce siderophores with high affinity for ferric iron. The irony of the ferritale is that iron is abundant in soil, but it is largely non available. Thus there is a fierce battle for iron in the rhizosphere that can result in suppression of soil- borne disease by siderophore producing pseudomonads. Between 1984 and 1994 and under the wings of Bob Schippers a group of, then, young scientists (Ron van Peer, Bert Bakker, Boet Glandorf, Ben Duijff, Jos Raaijmakers, Marcel Leeman, Willem-Jan de Kogel, and myself) worked on different aspects of the interactions between plants, fluorescent pseudomonads and plant pathogens. Induced systemic resistance (ISR) was discovered to be an important mode of action in suppression of disease by fluorescent pseudomonads (Van Peer et al., 1991; Leeman et al., 1995). The ferritale was also evident in the ISR story, as iron availability has a significant impact on the effectiveness of ISR (Leeman et al., 1996). The work on ISR was intensified when Kees van Loon started heading the Phytopathology group in 1992, and *Arabidopsis thaliana* was the new model system. Again iron came into play, as siderophores were among the multitude of bacterial elicitors of ISR (Meziane et al., 2005; Van Loon et al., 2008).

While working with Kees, field trials to study the impact of genetically modified pseudomonads on the rhizosphere microbiome were performed and methods to study the composition of root associated microbial communities were developed by Boet Glandorf (Glandorf et al., 2001), and Mareike Viebahn (viebahn et al., 2005) in cooperation with Karel Wernars and Eric Smit (National Institute of Health and the Environment). The DNA fingerprint techniques used at that time were amplified ribosomal DNA restriction analysis (ARDRA, Glandorf et al., 2001) and denaturing gradient gel electrophoresis (DGGE) of ribosomal DNA amplicons (Viebahn et al., 2005). DGGE was also used by Rogier Doornbos to study the impact of ISR and systemic acquired resistance (SAR) on the rhizosphere microbiome (Doornbos et al., 2011). The next step in studying the rhizosphere microbiome composition was the use of PhyloChip technology (Mendes et al., 2011; Berendsen et al., 2018). After Corné Pieterse became leader of the Plant-Microbe Interactions group, amplicon sequencing and shotgun metagenome sequencing replaced the previously mentioned methods. To my surprise the ferritale is ongoing in this age of high throughput analysis of plant root associated microbiomes. Arabidopsis roots excrete coumarins under iron deficient conditions and it was discovered that coumarins are important for microbiome assembly (Stringlis et al., 2018), but coumarins also significantly affect gene expression in root associated pseudomonas (Yu et al., 2021). Furthermore, coumarins are suggested to be the driving force for domestication of Pseudomonas in the rhizosphere of Arabidopsis (Li et al., 2021), and they play a pivotal role in the establishment of the soil-borne legacy (Vismans, 2022).

Peter Bakker met collega's en deelnemers aan het KNPV-symposium "From Plant Growth Promoting Rhizobacteria (PGPR) to Plant Microbiome" (foto: Hans van Pelt).



Bron: Bakker et al. (2020) Molecular Plant 13: 1395-1402.

Thus I think that the ferritale from the underground is alive and kicking and that there are ample opportunities for amazing discoveries. Always keep in mind that relevant questions and hypotheses that can be tested experimentally are the basic ingredients for good science.

I want to take the opportunity to thank the PMI group for the super good atmosphere. Johanna Westerdijk's motto "Werken en feesten vormt schoone geesten" (Work and partying creates beautiful minds) (Faasse, 2012) is kept alive until this day. It was a privilege to be part of this group for such a long time. Finally I want to thank the organizers of the symposium, Roeland Berendsen, Leo van Overbeek and Roland Willman, for a wonderful and exciting afternoon.

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