

## **MSc research project in the Plant-Microbe Interactions group (2021)**

**Plants live in complex environments in which they intimately interact with a broad range of insects and micro-organisms. World-wide, pathogenic microbes and insect herbivores cause major crop losses. However, plants are not helpless, as - like animals - they possess a sophisticated innate immune system that protects them against the majority of their attackers. Moreover, plants recruit beneficial microbes to their root microbiome that promote plant growth and stimulate the plant immune system.**

The research of the Plant-Microbe Interactions group (PMI) aims to explore and exploit the plant's natural immune system. We aim to understand how plant pathogens are able to infect plants and how resistant plants are able to defend themselves. We also investigate how beneficial microbes in the rhizosphere microbiome play a role in boosting the plant immune system and thereby stimulate plant health and growth. By investigating molecular and ecological aspects of plant innate immunity, infection, and rhizosphere microbiome biology, the PMI group aims to gain knowledge on how plants are able to cope with often hostile changes in their environment, and to utilize this knowledge for the development of novel strategies for (biological) crop protection. The research goals are being achieved by using the model plant species *Arabidopsis thaliana* and several crop species in combination with state-of-the-art techniques and methods in phytopathology, microbiology, molecular biology, biochemistry, genetics, genomics and bioinformatics.

### **Themes of the PMI group:**

- Induced systemic resistance (ISR) - Corné Pieterse
- Hormone crosstalk in plant immunity - Saskia Van Wees
- Genetics of disease susceptibility and pathogen infection - Guido Van den Ackerveken
- Microbial ecology of disease suppression by root microbiota - Peter Bakker
- Microbial (meta)genomics of plant-associated microbes - Ronnie de Jonge
- Recruitment of beneficial microbiomes - Roeland Berendsen

When you are interested in performing a MSc student research project in our group, please contact Corné Pieterse (C.M.J.Pieterse@uu.nl; if you want to orient yourself on which topic would suit you best), or any of the other staff members mentioned above.

Below a number of example projects that will become available soon:

**Project:** *Characterization of novel players in ABA- and JA-regulated plant defense*

**PMI sub-theme:** Prof. dr. Saskia van Wees

**Daily supervisor:** Niels Aerts (PhD candidate)

**Project description:**

Large parts of the plant immune system are regulated by plant hormones. Jasmonic acid (JA) and abscisic acid (ABA) regulate the part that promotes defense against insects and attenuates defense against necrotrophic pathogens. Additionally, ABA regulates responses to abiotic stresses such as drought and high salinity. Previously, we performed a high-throughput RNA-seq experiment with Arabidopsis that was treated with JA, ABA or a combination of the hormones and monitored the transcriptome over time. Using bioinformatics analyses, we predicted the importance of several transcription factors as novel players in the ABA and JA networks. The aim of this project is to characterize these novel players. This will be done with phenotypic experiments (monitoring defense- and drought-related phenotypes in mutants) and molecular experiments, such as qPCR, Yeast One-Hybrid and protoplast induction assays. Moreover, complementary subprojects involving bioinformatic analyses of transcriptome data are possible.

*Plant pathology · Insects · Drought · Hormones · Molecular biology · Bioinformatics*

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**Project:** *How robust is microbe-induced resistance in tomato under multi-attacker conditions?*

**PMI sub-theme:** Prof. dr. Saskia van Wees

**Daily supervisor:** Dharani Kamalachandran (PhD candidate)

**Project description:**

Root colonization by certain beneficial microbes can prime other plant parts to enhance their defense response against attack by a pathogen or insect. This type of microbe-induced protection is called Induced Systemic Resistance (ISR). The ISR response typically relies on priming of defense responses that are regulated by the plant hormones jasmonic acid (JA) and ethylene (ET), but some bacteria have been demonstrated to trigger systemic resistance via the salicylic acid (SA) signaling pathway. In this project, you will test the role of the hormones JA, ET and SA in ISR triggered by different bacteria in tomato plants against different pests and diseases. You will design and perform ISR bioassays, which involve tomato plant cultivation (wild type and hormone mutants), microbe and insect culturing, disease and pest measurements, and gene expression analyses by qPCR. You will also study the robustness of ISR: Are ISR-elicited plants still enhanced resistant when they face two different attackers, which are controlled by antagonistically acting hormone-mediated pathways? Therefore, you will compare the response of ISR-primed plants to single versus multiple attacker conditions.

*Plant pathology · Insects · Hormones · ISR · Tomato · Molecular biology*

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**Project:** *Studying translatability of microbe-induced resistance in tomato to agricultural practice conditions*

**PMI sub-theme:** Prof. dr. Saskia van Wees

**Daily supervisor:** Dharani Kamalachandran (PhD candidate)

**Project description:**

Application of microbe-induced systemic resistance (ISR) in agricultural practice can potentially make crops more resilient to pests, diseases and abiotic stresses like drought and shade. ISR can thus lead to increased yields while the use of harmful pesticides can be reduced. However, the translation of the ISR technology to agricultural practice largely depends on the reliability of ISR activity under different crop cultivation conditions. In this project, you will test the influence of the plant genotype, the growth substrate and a chosen abiotic stress on ISR against different insects and pathogens. You will design and perform ISR bioassays, which involve tomato plant cultivation (wild and domesticated tomato lines) in different substrates like soil and rockwool, microbe and insect culturing, application of an abiotic stress, disease and pest measurements, and gene expression analyses by qPCR. You will also study how various plant physiological parameters like biomass and stomatal conductance are influenced during the bioassays in different setups.

*Plant pathology · Insects · ISR · Tomato · Agriculture · Plant physiology · Molecular biology*

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**Project:** *Effects of biological seed coatings on root colonization patterns of mutualistic and pathogenic soil microbes.*

**PMI sub-theme:** Prof. dr. Saskia van Wees & Dr. Iannis Stringlis

**Daily supervisor:** Robin Cowper (PhD candidate)

**Project description:**

Coating of seeds improves the delivery of pesticides, nutrients, and growth promoters to the plant. Bioactive properties of microbes and their components can be exploited as sustainable and effective alternatives to the use of synthetic chemicals for seed coating. Soil inoculation with selected microbes can promote plant growth and can prime the plant immune system. However, little is known about the ability of microbes on seeds to promote plant health and resistance to stresses and how this is influenced by the plant's abiotic environment. In this project, we aim to evaluate the bioactive properties of a mushroom-forming saprophytic fungus, which we use to coat seeds. Specifically, I'm investigating whether the coating of seeds with different preparations of mycelium from the fungus is able to promote the growth, health and resistance in Arabidopsis and Tomato plants. This project contains studies using methods such as image analysis, confocal microscopy, plant phenotyping, gene expressions studies, as well as disease resistance assays. This research contributes towards developing the application of microbes as seed coating materials and biocontrol agents.

*Plant pathology · Disease assays · Plant phenotyping · Microscopy · Transcriptomics*

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**Project:** *Bioactive properties of biological seed coatings for Arabidopsis and Tomato.*

**PMI sub-theme:** Prof. dr. Saskia van Wees & Dr. Iannis Stringlis

**Daily supervisor:** Robin Cowper (PhD candidate)

**Project description:**

Soil inoculation with selected microbes can promote plant growth and can prime the plant immune system via the modulation of the host's transcriptional landscape. The efficient colonisation of roots by rhizosphere microbes is key in unlocking their beneficial mechanisms towards plants, and therefore in determining their efficacy in increasing plant growth and resistance to stress. However, root colonization requires a complex molecular dialogue between the beneficial microbe and the plant, as well as their interactions with other microbes in the rhizosphere. Currently, little is known about the ability of microbes and their metabolites to affect the outcome of the plant-microbe interaction. In this project, we plan to evaluate the bioactive properties of a saprophytic fungus, which we use to coat vegetable and Arabidopsis seeds. We want to know whether coated seeds can improve the root colonisation by a well-known plant-beneficial fungus, *Trichoderma harzianum* T-22. This saprophytic fungus secretes molecular cues so subvert plant defences and facilitate the colonisation of roots. First, we plan to observe changes in the root colonisation patterns by T-22. Additionally, we will study the interplay between seed coating and the plant immune system and whether that affects the plant's regulation of root colonization by T-22. Moreover, we aim to determine the effect of coating on resistance to pathogens and tolerance to nutrient stress.

*Plant pathology · Plant phenotyping · Microscopy · Transcriptomics*  
*· Microbiome analysis*

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**Project:** *Comparative competomics: searching for improved root colonization traits*

**PMI sub-theme:** Dr. Ronnie de Jonge

**Daily supervisor:** Juan Sanchez Gil (PhD candidate)

**Project description:**

In nature, many soil microbes can interact with plant roots and influence plant health. Some of these microbes provide beneficial services for the plant, like increase nutrient availability, activating immune processes and competing against pathogens. To do so, beneficial microbes need to develop mechanisms to colonize and persist in the root microbiome of the host plant. Among beneficial bacteria, *Pseudomonas* is a large and diverse genus that comprises many species of plant-associated bacteria.

In this project, we will look for the genes and functions that allow improved root colonization capabilities among natural root-associated *Pseudomonas* isolates. We will use sequencing information obtained from colonization experiments and study the genomes of those isolates that show improved colonization ability.

*Microbiology · Bioinformatics · Genomics · Ecology*

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**Project:** *Transcriptomics of root colonization - conquering the root microbiome*

**PMI sub-theme:** Dr. Ronnie de Jonge

**Daily supervisor:** Juan Sanchez Gil (PhD candidate)

**Project description:**

In nature, many soil microbes can interact with plant roots and influence plant health. Some of these microbes provide beneficial services for the plant, like increase nutrient availability, activating immune processes and competing against pathogens. To do so, beneficial microbes harbour mechanisms to colonize, compete and persist in the root microbiome of the host plant. However, little is known about the expression or functioning of these mechanisms in the natural context. In this project, we will study gene expression of known root-associated bacteria in the root environment and its microbiome. For this, we will generate metagenomes and metatranscriptomes that we will use to extract information of genes and pathways that determine the process of root colonization.

*Molecular biology · Transcriptomics · Bioinformatics · Ecology*

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**Project:** *The plant microbiome to the rescue: Soil-borne legacies improve plant health*

**PMI sub-theme:** Dr. Roeland Berendsen

**Daily supervisors:** Dr. Roeland Berendsen, Jelle Spooren

**Project description**

Plant roots accommodate an astonishing abundance and diversity of microbes. These microbes can either negatively affect the plant by causing disease, or positively by promoting plant health and growth. Plants exude significant amounts of metabolites into the soil to nourish the microbial communities that live around the roots. When a plant is stressed by for example a pathogen, it can 'cry for help' and alter the blend of metabolites that it releases into the soil in such a way that it specifically attracts certain beneficial microbes. These microbes can exploit these metabolites and in return they stimulate the plants immune system, thereby combatting the pathogen. Recently we found that these beneficial microbes can persist in the soil as a soil-borne legacy of disease, thereby protecting a second generation of plants growing in the same soil. Although this has great potential as a sustainable alternative for the use of pesticides in agriculture, as of yet a lot of questions remain. In this research, we aim to unravel which beneficial soil microbes are recruited by the plant when it is infected above ground, and through which metabolites this recruitment takes place.

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**Project:** *How does a plant cry for help upon pathogen infection?*

**PMI sub-theme:** Prof. Saskia van Wees

**Daily supervisor:** Run Qi

**Project description**

Being part of the project described above, I mainly focus on the plant part, *Arabidopsis*, investigating what are the cry-for-help genes, how are these genes initially triggered and regulated, what does the plant exactly gain from cry-for-help. Students who are interested in plant-pathogen interactions, plant systemic signal transduction, and like to perform bioassays, and/or molecular work, and/or get acquainted with bioinformatics (analysis of transcriptome) are encouraged to contact us..

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**Project: *Digging into the ‘soy-borne legacy’: the who, what and how of microbiome-mediated host protection***

**PMI sub-theme:** Dr. Roeland Berendsen

**Daily supervisor:** Sietske van Bentum (PhD candidate)

**Project description:**

Plants are able to shape the composition of their root microbiome under certain circumstances. Our lab has previously shown that aboveground infection of *Arabidopsis thaliana* leaves with downy mildew results in increased abundance of specific bacterial strains in the root microbiome. These bacteria were shown to protect healthy plants against infection by downy mildew in a ‘soil-borne legacy’. Plant disease can thus act as a trigger for plants to select specific beneficial microbes in the root environment. In this project, we study whether a crop plant (soybean) can activate similar processes upon disease. We want to know if what kind of microbes are recruited by the plant, if these microbes can protect soybean against disease, and how soybean recruits these microbes specifically upon disease. You will use DNA sequencing to compare the root microbiome composition of healthy and diseased plants, isolate candidate beneficial microbes by selective plating and design + execute experiments to understand the mechanism underlying plant-mediated changes in the root microbiome.

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**Project: *Microbial modulation of plant root defenses to convince a plant to become a host***

**PMI sub-theme:** Dr. Roeland Berendsen

**Daily supervisor:** Sietske van Bentum (PhD candidate)

**Project description:**

Plants are colonized by a plethora of microbes in the rhizosphere, the narrow zone of soil surrounding plant roots. These root-colonizing microbes have adapted to this plant-governed environment that includes general plant defenses. The mechanisms of suppression of plant defenses by root-colonizing microbes is still poorly understood. Recent work in our lab with various root-colonizing bacteria (including the beneficials *Pseudomonas simiae* WCS417 and *P. capeferrum* WCS358) has shown that induction of three plant defense genes in the roots is suppressed via bacterial modulation of extracellular pH. In this project, we want to know whether three bacteria isolated from diseased plants also suppress host defense gene expression in a similar manner. These three bacteria were previously isolated from the rhizosphere of *Arabidopsis thaliana* and shown to protect *A. thaliana* as a consortium against aboveground infection with downy mildew. Based on your first results, you will design and execute follow-up experiments to understand in great detail how such beneficial, root-colonizing microbes successfully interact with plant roots.

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**Project: *The arbuscular mycorrhizabiome*****PMI sub-theme:** Dr. Roeland Berendsen**Daily supervisors:** Dr. Roeland Berendsen, Changfeng Zhang (PhD student)**Project description**

Arbuscular mycorrhizal fungi (AMF) form symbiosis with 80% of terrestrial plants (Brundrett 2004) and have great impact on plant performance (Van Der Heijden *et al.* 1998; Bender *et al.* 2014). AMF are always surrounded by complex microbial communities, which modulate the mycorrhizal symbiosis. Here, we focus on microbial communities that synergistically attach to AMF. We hypothesize that mycorrhiza-associated microbes have beneficial functional traits from which both the mycorrhiza and the plant benefit. Whereas previous works describe single bacterial strains interacting with AMF (Artursson, Finlay and Jansson 2006), here, we aim to decipher the mycorrhizosphere microbial community by employing next-generation sequencing techniques. Moreover, we have built an extensive microbial collection of mycorrhiza-associated microbes. In this project, we will test these microbes for their effect on the mycorrhizal symbiosis.

**References**

- Artursson V, Finlay RD, Jansson JK. Interactions between arbuscular mycorrhizal fungi and bacteria and their potential for stimulating plant growth. *Environ Microbiol* 2006;**8**:1–10.
- Bender SF, Plantinga F, Nefstel A *et al.* Symbiotic relationships between soil fungi and plants reduce N<sub>2</sub>O emissions from soil. *ISME J* 2014;**8**:1336–45.
- Van Der Heijden MGA, Klironomos JN, Ursic M *et al.* Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 1998;**396**:69–72.
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**Project: *Natural microbial breeding for rhizosphere competence*****PMI sub-theme:** Dr. Ronnie de Jonge**Daily supervisor:** Sanne Poppeliers (PhD candidate)**Project description:**

Naturally, plants roots live in association with countless microbes, also known as the *root microbiome*. The root-associated microbiome is not only essential for plant functioning, but plant species are able to ‘engineer’ these communities - often to their benefit - by attracting microbes using specific root exudates. A lot of work has been done to discover beneficial microbes and bioinoculants that can provide plants with important services like growth promotion or pest control. While these studies look promising under controlled conditions, bioinoculant success varies widely in the field. In this project, we will look for genes and/or pathways that make a microbe rhizosphere competent by using so-called experimental evolution. We will inoculate bioinoculants on plants grown under natural, non-sterile conditions. After a four-week growth cycle, the total rhizosphere population is harvested, filtered for the bioinoculant through means of antibiotic and/or fluorescent marker selection, and transferred to new plants. This process will be repeated at least four times to monitor the “evolution” of the introduced bioinoculant over time in the rhizosphere. We will use metagenome sequencing to determine, over time, the frequency of beneficial microbe single nucleotide polymorphisms (SNPs). The impact of the identified SNPs on microbial processes will be assessed through computational analysis.

*Microbiology · Experimental evolution · Bioinformatics · Genomics*

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**Project:** *Community ecology of root-associated bacteria over time*

**PMI sub-theme:** Dr. Ronnie de Jonge

**Daily supervisor:** Sanne Poppeliers (PhD candidate)

**Project description:**

Naturally, plants roots live in association with countless microbes, also known as the root microbiome. Plant species are able to ‘engineer’ these communities by attracting microbes using specific root exudates. However, we still lack a mechanistic understanding of ecological community assembly processes that are important in this environment. Apart from correlations between microbial community composition and specific environmental parameters or plant species, we still don’t know much about what really drives microbial community assembly in the rhizosphere, what niches bioinoculants (can) occupy, and how we could manipulate all this. In this project we will study (ecological) aspects of rhizosphere microbial community assembly over time, and how this might be influenced by the introduction of beneficial bacteria. We will do experiments with *Arabidopsis thaliana* in natural soil and follow the microbial communities over time using 16S amplicon and metagenome sequencing. Based on results of initial experiments, we will design and execute follow-up experiments to understand and validate how microbial community assembly in the rhizosphere works and how these processes are influenced by the introduction of beneficial bacteria.

*Microbial community ecology · Bioinformatics · Genomics*

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**Project:** *Role of coumarins in the microbiome-root-shoot axis*

**PMI sub-theme:** Prof. Corné Pieterse / Dr. Giannis Stringlis

**Daily supervisor:** Dr. Giannis Stringlis (post doc)

**Project description:**

Plant roots release diverse compounds (exudates) that mediate plant communication with the root-associated microbiome but also mediate nutrient uptake from the soil. Coumarins are among these exudates and they have a well-established role in iron uptake from the soils where this nutrient is unavailable. Recent evidence suggests that coumarins have a selective role in the rhizosphere, since beneficial microbes are tolerant to coumarin scopoletin, while selected pathogenic microbes are sensitive. Coumarins accumulate in the roots in response to colonization by beneficial microbes. Interestingly, some plant mutants that have a role in coumarin accumulation/exudation are unable to show induced systemic resistance (ISR) following colonization by beneficial microbes. The goal of this project is to characterize the spatial accumulation of coumarins in roots and leaves of plants colonized by beneficial rhizobacteria (gene expression, metabolomics) and the role of coumarin biosynthesis- and ISR-related genes in the communication of roots and shoots (micrografting, ISR experiments).

*Plant gene expression · metabolomics · micrografting*

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**Project: *Structural and chemical defense components in the root: Gatekeepers of microbial colonization!***

**PMI sub-theme:** Prof. Corné Pieterse / Dr. Giannis Stringlis

**Daily supervisor:** Melissa Uribe Acosta (PhD student)

**Project description:**

Plants are growing in close association with a plethora of microbes, collectively known as the microbiome. Members of the microbiome can be beneficial for plant growth and health, but there are also microbes that can cause disease to plants. For this reason, plants have developed diverse defense strategies to control invasion by pathogens. The first line of plant defense relies on structural fortification of the cells (lignification, deposition of callose, suberization) and the release of chemicals with antimicrobial activity (glucosinolates, coumarins, camalexin). While the role of these defense components is well-characterized in the leaves of plants, their role in the protection of the root by unwanted invaders is limited. In this project, we will use mutants for different defense components and assess their role in root colonization by beneficial and pathogenic microbes. We will also assess how different mutations can affect the release of exudates and the transcriptional responses activated following colonization by testing root defense marker genes.

*Plant gene expression · metabolomics · disease assays*

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**Project: *How do effector proteins, the weapons of plant pathogenic microbes, manipulate host plants?***

**PMI sub-theme:** Prof. Dr. Guido Van den Ackerveken

**Daily supervisor:** Sebastian Tonn (PhD candidate)

**Project description:**

Effectors are proteins that are secreted by plant pathogens and that contribute, in many different ways, to a successful infection of the host plant. There are diverse known functions of effectors, from acting as a shield protecting the pathogen against harmful plant enzymes to suppressing the plants defense signaling pathways. But for many effectors their exact function is still unknown. Understanding how plant pathogens manipulate their hosts will help to develop better strategies to protect crop plants.

In this project we want to study the function of effectors of the lettuce downy mildew pathogen *Bremia lactucae*. In previous projects we identified effectors that are expressed during the infection but for most of them, we do not know if and how they contribute to successful infection.

The methods to study this particular plant-pathogen interaction are limited by the obligate biotrophic lifestyle of *B. lactucae*: it cannot be cultured in vitro on artificial growth media. Therefore, powerful methods like genetic transformation are not available.

However, recently developed tools like nanoparticle mediated transient transformation or smallRNA-mediated gene silencing have the potential to enable us to study the pathogen more directly. For example, such tools could be used to suppress the expression of certain effectors (or other genes) during infection and then to check if that has an impact on the pathogen.

We would like to combine these novel tools with established methods based on *Agrobacterium*-mediated transient transformation to find out how *B. lactucae* effectors manipulate plants and how important they are for successful infection.

*Plant Pathology · Plant Immunity · Effectors · Molecular Genetics · Biotechnology*

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**Project: Study of the recognition of bacterial flagellin in lettuce for improved disease resistance and food safety**

**PMI sub-theme:** Prof. Dr. Guido Van den Ackerveken

**Daily supervisor:** Dmitry Lapin (postdoctoral researcher)

Bacterial diseases and contaminations result in vegetable crop losses and food poisonings. Causal bacteria often have flagella for their motility in the environment. Although a flagellin peptide coming from flagella can trigger effective immune responses in plants, certain bacteria escape the recognition by adjusting the peptide sequence. In this project, you will mine natural allelic variation of lettuce to find forms of the flagellin receptor that recognize different flagellin variants. You will clone the receptor variants from a diverse set of lettuce varieties and analyze their capacity to react to selected variants of bacterial flagellin using reactive oxygen species (ROS) burst assays. Finally, you will test how this recognition helps to restrict growth of unwanted bacteria. This work should provide a better understanding of the bacteria perception in lettuce and form a technological basis for the quick identification of receptors to control the growth of specific groups of bacteria in plants.

*Immunology · Pathogen perception · Crop design · Disease resistance · Cloning*

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**Project: Detection of the early downy mildew infection by lettuce plants**

**PMI sub-theme:** Prof. Dr. Guido Van den Ackerveken

**Daily supervisor:** Dmitry Lapin (postdoctoral researcher)

Downy mildew diseases caused by obligate oomycete pathogens pose a significant threat for a broad range of crops. However, what molecular patterns these microbes produce and how plants detect them is poorly understood. The project aims to identify genetic factors mediating sensing of the initial downy mildew infection process in plants. For this, you will capitalize on a collection of ~400 lines from wild and domesticated lettuce species that differ in the ability to resist downy mildew. You will analyze the perception of extracts from the gnotobiotic culture of lettuce downy mildew using the reactive oxygen species burst assays. Combined with the phylogeny of lettuce species, association mapping will help you to learn about the genetic basis of downy mildew perception and its evolution.

*Immunology · Pathogen perception · Receptor · GWAS · Genetics*

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**Project: *Mapping SynCom dynamics in Arabidopsis***

**PMI sub-theme:** Dr. Ronnie de Jonge

**Daily supervisor:** Gijs Selten (PhD candidate)

**Project Description:** Here at PMI, we have established a bacterial collection isolated from the rhizosphere and endosphere of *Arabidopsis thaliana* Col-0 and the coumarin production mutant myb72 grown in natural soil. These bacterial isolates can be assembled into Synthetic Communities (SynComs) which we can inoculate with Arabidopsis to study the interactions between plant and microbes. This way, we are looking at a simplified but representative natural root microbiome within a gnotobiotic and controllable system. In this project we will use this bacterial collection to create SynComs that we inoculate with Arabidopsis to study the dynamics of the bacteria in the root microbiome. Different approaches are inoculating different SynCom compositions with Arabidopsis or under different environmental conditions and/or stresses. In combination with bioinformatic analyses, we might find interesting genes and functions of bacteria involved in root colonization. Based on these findings, we can then design more (SynCom) experiments by inclusion or exclusion experiments of specific bacteria, or by mutating bacterial genes to research these potential bacteria-plant interactions more closely.

*Microbiology – Ecology – Bioinformatics – Genetics*

!! Project starts in November 2021 at the earliest !!

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