TECHNISCHE UNIVERSITÄT MÜNCHEN

TUM School of Life Sciences

From plant immunity to microbiome dynamics in the phyllosphere

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Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung des akademischen Grades einer Doktorin der Naturwissenschaften genehmigten Dissertation.

Vorsitz: apl. Prof. Dr. Matthias Ehrmann

Prüfende der Dissertation:

1. Prof. Dr. Jörg Durner

2. Prof. Dr. Michael Schloter

Die Dissertation wurde am 02.09.2024 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 20.11.2024 angenommen.

PUBLICATIONS RELATED TO THIS THESIS:

Sommer, A., Wenig, M., Knappe, C., Kublik, S., Foesel, B.U., Schloter, M. et al. (2024) **A salicylic acid-associated plant-microbe interaction attracts beneficial *Flavobacterium* sp. to the *Arabidopsis thaliana* phyllosphere**. *Physiologia Plantarum*, 176(4), e14483. https://doi.org/10.1111/ppl.14483

Alessandro Brambilla, Anna Sommer, Andrea Ghirardo, Marion Wenig, Claudia Knappe, Baris Weber, Melissa Amesmaier, Miriam Lenk, Jörg-Peter Schnitzler, A Corina Vlot, **Immunity-associated volatile emissions of β-ionone and nonanal propagate defence responses in neighbouring barley plants**, *Journal of Experimental Botany*, Volume 73, Issue 2, 13 January 2022, Pages 615–630, https://doi.org/10.1093/jxb/erab520

Vlot, A.C., Sales, J.H., Lenk, M., Bauer, K., Brambilla, A., Sommer, A., Chen, Y., Wenig, M. and Nayem, S. (2021), **Systemic propagation of immunity in plants**. New Phytol, 229: 1234-1250. https://doi.org/10.1111/nph.16953

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SUMMARY

Plants face constant threats by pathogens and pests. Thus, they have evolved intricate immune responses to react to those biotic stressors as well as to abiotic stressors like drought and heat in an adequate manner. They interact closely with their microbiome to regulate and fine-tune those reactions. One of the strategies to react to pathogenic threats is the priming of plant immunity, elicited by beneficial microbes usually associated with the roots: so-called plant growth promoting rhizobacteria and fungi (PGPR/F). Those are capable of inducing mainly epigenetic changes and minute direct changes in gene expression to bring the plant into a ready state to be able to react fast and strong upon pathogenic challenge without compromising plant growth in the absence of pathogens. This elicitation of immune priming by beneficial bacteria is called PGPR/F induced resistance (PGPR/F IR).

In this treatise, I was able to show that *Bacillus thuringiensis* (*Bt*) is capable of raising systemic immunity in the plant if applied to the roots. This *Bt* IR is dependent on jasmonic acid as well as salicylic acid signaling via priming of immune responses. I also followed the question if PGPR IR would induce changes in the microbial composition of the phyllosphere. *Bt* itself is not capable of proliferating in the phyllosphere. Microbial changes in the phyllosphere upon *Bt* treatment are minute and not significant. Thus, I can conclude that classical PGPR IR, mostly conferred by priming, does not trigger meaningful changes in the phyllosphere microbiome.

In addition, I introduced a novel inoculation approach to a well-known and researched PGPR IR inducing bacterial strain, *Pseudomonas simiae* WCS417r (WCS417). I was able to show that root-dipping instead of soil-drenching was also capable to elicit IR, albeit presumably in a different manner than the soil-drenching method: In addition to thriving at the roots, WCS417 was also capable of reaching and proliferating in the phyllosphere, i.e. the habitat on the leaves. The resulting immunity response differed from the classical immunity response reported so far: It was dependent on jasmonic acid signaling as had been reported before, but additionally, it was dependent on salicylic acid and pipecolic acid signaling. This might be due to an additional interaction with the plant's immune status at the site of the leaves.

In regard to the phyllosphere microbiome, WCS417 root-dip treatment led to proliferation of WCS417 on the leaves, and also to an enrichment of a *Flavomonas*

johnsoniae strain in a microbe-plant-microbe interaction dependent on the plant-signaling hub NPR1. *F. johnsoniae* is capable of inducing a systemic SAR-like immune response as well as increasing plant growth in applied to the leaves, thus further heightening the plant resistance in addition to PGPR IR by WCS417.

ZUSAMMENFASSUNG

Pflanzen als sessile Organismen haben sich im Laufe der Evolution derart entwickelt, dass sie sich in hohem Maße an wechselnde Umweltbedingungen anpassen können. Zu diesen Umweltfaktoren gehören unter anderem biotische Stressoren aller Art, seien es Insekten, Viren, bakterielle oder mykotische Krankheitserreger oder eukaryotische Pathogene. Pflanzen haben komplexe Regulationsmechanismen entwickelt, um auf diese Bedrohungen adäquat zu reagieren. Einer dieser Mechanismen ist die so genannte Induzierte Resistenz (IR), welche früher auch als ISR bezeichnet wurde. Bei der IR erlangen Pflanzen eine erhöhte Resistenz, die durch nützliche Mikroben wie Bakterien oder Pilze, die hauptsächlich im Boden und in der Rhizosphäre leben, vermittelt wird. Diese Resistenz kann je nach der auslösenden Art von Mikroorganismus gegen verschiedene Herausforderungen wirksam sein, z. B. gegen biotrophe oder nekrotrophe bakterielle oder virale Krankheitserreger, Insekten oder sogar abiotische Stressfaktoren wie Trockenheit. Das bisher am besten untersuchte IR-System ist die von *Pseudomonas simiae* WCS417r (WCS417) in *Arabidopsis thaliana* ausgelöste IR gegen das Pathogen *Pseudomonas syringae* pathovar *Tomato* DC3000 (*Pst*). Bislang ging man davon aus, dass diese Ausprägung von IR unabhängig von Salicylsäure-Signalen ist und nur von Jasmonsäure Derivaten in der Signalkaskade abhängt. In dieser Studie präsentiere ich Hinweise dafür, dass Salicylsäure möglicherweise doch eine wichtige Rolle bei der Signalgebung dieses IR-Systems spielt. Darüber hinaus zeige ich, dass *Bacillus thuringiensis* (*Bt*), ein Bakterienstamm, welcher hauptsächlich für seine insektiziden Eigenschaften bekannt ist, ebenfalls IR in *Arabidopsis* auslöst. Diese IR ist ebenfalls von SA und Jasmonaten abhängig. In dieser Studie beleuchte ich auch weitere Komponenten der Signalkaskade.

Pflanzen entwickelten sich in enger Gemeinschaft mit den Mikroben ihrer Umgebung, und so wurde die Holobionten-Theorie entwickelt, um die Pflanze als einen komplexen Organismus zu beschreiben, dessen phänotypische Eigenschaften nicht nur durch die Pflanze selbst, sondern auch durch sein Mikrobiom ausgeprägt werden, welches zur Anpassung an die Umwelt und zur Fitness des Wirtes beiträgt. Beide Elemente, sowohl die Pflanze als auch das Mikrobiom, haben sich gemeinsam entwickelt, um sich an die Herausforderungen der Umgebung anzupassen. Diesem Konzept folgend habe ich das Mikrobiom der Blätter von *Arabidopsis* untersucht, nachdem entweder mit

WCS417 oder *Bt* eine IR induziert wurde. Und tatsächlich konnte ich charakteristische Veränderungen in der Zusammensetzung des Mikrobioms der Phyllosphäre nachweisen. Dazu gehört die Reduktion potenziell schädlicher Bakterien und die Anreicherung nützlicher Bakterien. In *Arabidopsis* gehören dazu Bakterienstämme, die mit wachstumsfördernden und resistenzfördernden Eigenschaften in Verbindung gebracht werden. Weiterführende Experimente mit einem dieser Bakterienstämme konnten zeigen, dass dieser in der Lage war, eine SAR-ähnliche systemische Immunität hervorzurufen.

ABBREVIATIONS

As well as SI units, metric prefixes, and the abbreviations for nucleotides, the following abbreviations were used in this work:

ABA	**Abscisic acid**
ABA-GE	**β-D-Glucopyranosyl abscisate**
ABC-G (transporter)	**ATP-binding cassette transporter, subfamily G**
ALD1	**AGD2-LIKE DEFENCE RESPONSE PROTEIN 1**
ASV	**Amplicon Sequence Variant**
AzA	**Azelaic acid**
AZI1	**AZELAIC ACID INDUCED 1**
BAK1	**BRASSINOSTEROID INSENSITIVE 1-associated receptor kinase 1**
BKK1	**BAK1-LIKE1**
Blast	**Basic local alignment search tool**
bp	**base pair(s)**
Bt	***Bacillus thuringiensis***
CERK1	**CHITIN ELICITOR RECEPTOR KINASE 1**
cfu	**colony forming units**
COI1	**CORONATINE INSENSITIVE 1**
d	**day(s)**
DNA	**Desoxyribonucleic acid**
dpi	**days post inoculation**
EARLI1	**EARLY ARABIDOPSIS ALUMINUM INDUCED 1**
EIL3	**ETHYLENE-INSENSITIVE3-LIKE 3**
EIN3	**ETHYLENE-INSENSITIVE3**

ERF-1	**ETHYLENE RESPONSIVE ELEMENT BINDING FACTOR 1**
ET	**Ethylene**
ETI	**Effector-triggered immunity**
ETS	**Effector triggered susceptibility**
FLD	**FLOWERING LOCUS D**
FLG22	**Flagellin fragment**
FLS2	**FLAGELLIN SENSITIVE 2**
FMO1	**FLAVIN-DEPENDENT MONOOXYGENASE 1**
GGPPS12	**GERANYL(GERANYL)DIPHOSPHATE SYNTHASE 12**
hpi	**hours past infection**
HR	**Hypersensitive Response**
ICS1	**ISOCHORISMATE SYNTHASE 1**
IR	**Induced Resistance**
ISR	**Induced Systemic Resistance**
ITS	**Internal transcribed spacer**
JA	**Jasmonic acid**
JA-Ile	**JA-Isoleucine**
JAR1	**JASMONATE RESISTANT 1**
JAZ	**JASMONATE-ZIM-DOMAIN PROTEIN 1**
JIN1	**JASMONATE INSENSITIVE 1**
LLP1	**LEGUME LECTIN-LIKE PROTEIN 1**
LOX	**LIPOXYGENASE 1**
MAMP	**Microbe-associated molecular pattern**
MeJA	**Methyl jasmonate**

MeSa	**Methyl salicylate**
min	**minute(s)**
MIN7	**HOPM INTERACTOR 7**
MPK	**Mitogen-activated protein kinase**
NB medium	**Nutrient broth medium**
NHP	**N-Hydroxypipecolic acid**
NO	**Nitric oxide**
NPR1	**NONEXPRESSER OF PR GENES 1**
OMF	**Orchid mycorrhizal fungi**
ORA59	**OCTADECANOID-RESPONSIVE ARABIDOPSIS 59**
PAL	**Phenylalanine ammonia-lyase**
PAMP	**pathogen-associated molecular pattern**
PCR	**Polymerase chain reaction**
PDF1.2	**PLANT DEFENSIN 1.2**
PGPF	**Plant Growth Promoting Fungi**
PGPR	**Plant Growth Promoting Rhizobacteria**
Pip	**Pipecolic acid**
PR1/4/5	**PATHOGENESIS-RELATED 1/ 4 /5**
Pst	***Pseudomonas syringae* pathovar *Tomato* DC3000**
PTI	**Pathogen-triggered immunity**
PYL6	**PYR1-LIKE 6**
RBOHD	**RESPIRATORY BURST OXIDASE HOMOLOGUE D**
RNA	**Ribonucleic acid**
RNAseq	**RNA sequencing**

ROS	**Reactive oxygen species**
rpm	**revolutions per minute**
RQ	**relative quantification**
SA	**Salicylic acid**
SAG	**SA 2-O-β-d-glucose**
SAR	**Systemic Acquired Resistance**
SARD4	**SAR-DEFICIENT4**
sec	**second(s)**
SID2	**SALICYLIC ACID INDUCTION DEFICIENT 2**
T3SS	**Type III secretion system**
TF	**Transcription factor**
UGT76B1	**UDP-DEPENDENT GLYCOSYLTRANSFERASE 76B1**
VOC	**Volatile Organic Compound**
VSP1/VSP2	**VEGETATIVE STORAGE PROTEIN 1/2**
WCS417	***Pseudomonas simiae* WCS417r**

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1. INTRODUCTION

Plants are sessile organisms and as such not able to evade adverse environmental factors by just moving somewhere else. Instead, they can perceive and adapt to various challenging surroundings. This is achieved on the one hand by alterations of gene expression patterns by the plant itself, and on the other hand by interactions with the plant's microbiome, which helps to finetune and balance responses to environmental cues via tightly controlled microbe-plant interactions. In the following paragraphs, I will shed light on the plant's microbiome and its role in plant defence against pathogens, followed by a more detailed explanation of the plant's innate immune system. I will also introduce the most important plant hormones and signaling molecules involved in plant defence against pathogens.

1.1 PLANT MICROBIOME

The plant microbiome is a vital part of the plant's health. It comprises all bacteria, fungi, archaea, protista, and viruses living on and in the plant, colonizing the different plant organs such as roots, leaves, flowers, and seeds. Some scientists hold the opinion that plants and their microbial companions evolved together as a so-called holobiont (Rosenberg & Zilber-Rosenberg, 2016). The microbiome helps the plant to adapt faster to adverse situations than regular evolution would allow. On the one hand, this is achieved by expanding and externalising metabolic functions by utilizing the microbiomes capabilities. On the other hand, the microbiome can help to adapt to adverse environmental conditions by interacting with the plant via signaling cues such as plant hormones and volatile organic compounds (Ravanbakhsh, Sasidharan, Voesenek, Kowalchuk, & Jousset, 2018; C. M. Ryu et al., 2004). This "external" set of genes for metabolic functions and regulation can be actively changed and adapted by the plants according to changing environmental cues, as the "cry-for-help" (see below) vividly shows. Thus, it is imperative to study plants in the bigger context of the holobiont, i.e. plant plus microorganisms, in order to gain a full understanding of how the plant copes with biotic as well as abiotic stressors in its environment (Hassani, Durán, & Hacquard, 2018; Mesny, Hacquard, & Thomma, 2023; Rosenberg & Zilber-

Rosenberg, 2016). Plants and bacteria can even exchange genes via horizontal gene transfer, which has been proven, for example, for genes involved in auxin synthesis (Haimlich, Fridman, Khandal, Savaldi-Goldstein, & Levy, 2024). To study the plant isolated from its microbiome means turning a blind eye on a big part of the organism. Studies have shown that the microbiome – especially that of the rhizosphere - can alter the phenotype of the plants. This includes for example, the timepoint of flowering: if the microbiome of an Arabidopsis ecotype of a late flowering phenotype is transferred to Arabidopsis ecotypes of early flowering, the time point of flowering shifts to a later time point and the biomass of the inflorescence increases, thus increasing the reproduction success (Panke-Buisse, Poole, Goodrich, Ley, & Kao-Kniffin, 2015). A well-known illustration of the influence of the microbiome on its host is the nitrogen fixation by microbial symbionts in the nodules of certain plant species, including Leguminosae. This enables the plant to grow and thrive in nitrogen-poor soils (Parniske, 2018). It is, however, noteworthy, that a considerable amount of nitrogen is actually fixed by non-symbiont microbes in the soil (Ladha et al., 2022). An extreme illustration of the importance of the plant microbiome for host fitness is obligate symbiosis, which is quite common in orchids: most orchids depend on orchid mycorrhizal fungi (OMF) at least for the germination of the seed (D. Wang, Jacquemyn, Gomes, Vos, & Merckx, 2021): They live as myco-heterotrophs, i.e. depending on specialised fungi to provide nutrients to the very small seeds, which are not viable on their own (Rasmussen, 1995). At least several species of orchids even remain obligate symbionts with their OMF for their whole lifecycle and don't fix carbon via photosynthesis at all (Bidartondo, 2005).

The plant's microbiome can additionally alter phenotypic traits such as drought tolerance, root architecture or, most important for this thesis: pathogen resistance (P. A. H. M. Bakker, Ran, Pieterse, & van Loon, 2003; Hubbard, Germida, & Vujanovic, 2014; Nagabhyru, Dinkins, Wood, Bacon, & Schardl, 2013; Sharifi, Jeon, & Ryu, 2021; Sherameti, Tripathi, Varma, & Oelmüller, 2008; Teixeira, Colaianni, Fitzpatrick, & Dangl, 2019).

Plants provide their offspring with a kind of "starter-pack" of microbes, which reside directly in the seed. Thus, positive traits can be vertically inherited, and the newly developing plantlet is more resilient to adverse environmental factors and can grow faster (Berg & Raaijmakers, 2018; Rybakova et al., 2017; Shade, Jacques, & Barret, 2017). Bziuk *et al.* were able to show that there is a significant connection between the genotype of barley and its seed microbiome. In addition, many bacteria of the seed

microbiome possess genes associated with plant beneficial traits including IAA production, siderophore release, or anti-microbial properties to fend off other, potentially pathogenic microbes (Bziuk et al., 2021). The authors even propose a connection between the ability of the plant of being primed by beneficial microbes against pathogens (see 1.2.2 Systemic immunity) and the microbial diversity of the seed microbiome (Bziuk et al., 2021; Wehner et al., 2019).

1.2 FACTORS SHAPING THE PLANT MICROBIOME

Beyond seeds having their own distinct microbiome, every plant organ, be it flower, root or leaf develops their own, specialised microbiome which can actively be shaped by the plant (Massoni et al., 2020; Massoni, Bortfeld-Miller, Widmer, & Vorholt Julia, 2021). Contributing to the microbial composition, aside from the plant organ is the plant species as well as it's specific genotype. This is especially drastic in genotypes deficient in parts of the innate immune system, but also holds true for different, healthy genotypes (Bodenhausen, Bortfeld-Miller, Ackermann, & Vorholt, 2014; Hacquard, Spaepen, Garrido-Oter, & Schulze-Lefert, 2017). Also, the developmental stage of the plant is exerts influence on the microbial composition (Chaparro, Badri, & Vivanco, 2014; Xiong et al., 2021). It could be shown that perennial plants develop a similar microbiome in subsequent years depending on the location. The differences in microbial composition are bigger between different seasons within one year than in the same season between different years. This hints to a microbiome composition tightly controlled by plant-microbe and microbe-microbe interactions which enable similar communities to evolve time and time again (Grady, Sorensen, Stopnisek, Guittar, & Shade, 2019; Redford & Fierer, 2009).

The microbiome of a plant is strongly affected by the microbiome of the soil, since it harbours a huge reservoir of different microbial species. In addition, wind, rain and insects are important sources for the diversity of microbiomes (Figure 1) (Bulgarelli et al., 2012; Julia A. Vorholt, 2012).

The microorganisms in the plant's microbiome include bacteria, fungi, oomycetes and other eukaryotic single-celled organisms as well as viruses. Whether Archaea play a major role in microbiome dynamics and are abundant or rather not, is not yet clear.

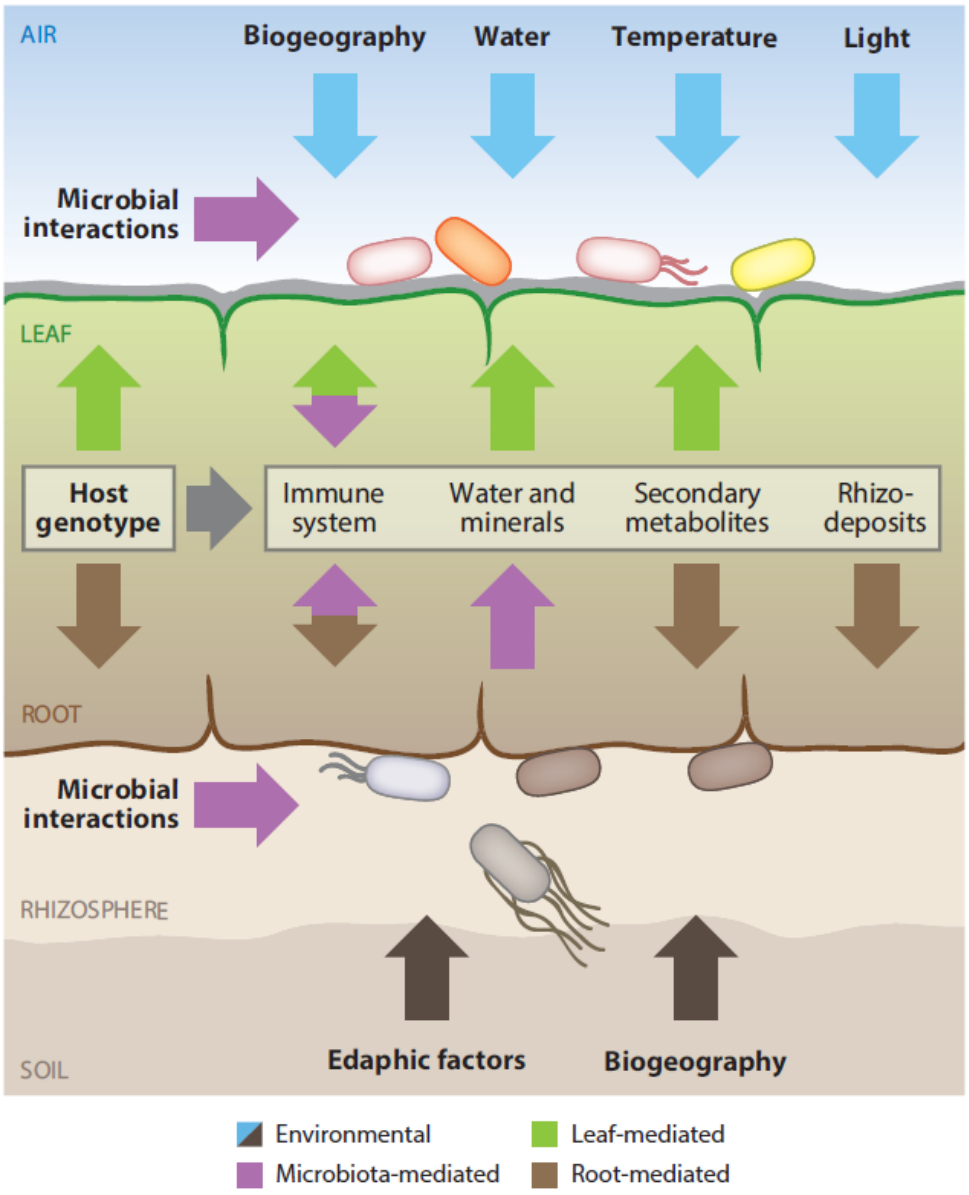

Figure 1: Factors influencing plant microbiome.

On the one hand, the microbial composition depends on external factors such as water availability, temperature, UV radiation, and oxygen availability. On the other hand, the microbiome is controlled by the plants through provision with carbon sources, secretion of secondary metabolites and the overall genotype. A third factor shaping the microbial composition around the plant are direct microbe-microbe interactions. Adapted from Müller et al. 2016

Different opinions and data points exist on that topic (Hassani et al., 2018; Y. Lu & Conrad, 2005; D. B. Müller, Vogel, Bai, & Vorholt, 2016; Julia A. Vorholt, 2012) Microbe-microbe interactions within the microbiome are major factors contributing to its composition. Certain “hub” species have a substantial influence on the remaining

microbial strains. This is especially pronounced in the presence of pathogens, which seem to lead to a reduction in microbial diversity (Agler et al., 2016; Jakuschkin et al., 2016; Rezki et al., 2016). Viruses which infect bacteria, so-called phages, have a discernible impact on the plant's microbiome by lowering bacterial load and increasing bacterial diversity as well as fluctuation in microbiome composition (Koskella & Taylor, 2018).

Microorganisms can not only dwell on the surface of the plant but thrive in even closer contact within plant tissues. This habitat and its microbiome is termed the endosphere. It is characterized by tightly controlled numbers and species of microbes which differ between the tissues of different plant organs (Stéphane Compant, Clément, & Sessitsch, 2010). Bacteria have been reported to mainly live in intercellular spaces, however, some strains have been found to also colonize intracellular spaces (S. Compant et al., 2008). In the leaves, bacteria can for example reside in intercellular spaces like substomatal chambers, parenchyma and the vascular system (Stéphane Compant et al., 2021).

1.3 Microbiome of the rhizosphere

The best studied microbiome of a specific plant organ is that of the root. The microbes can either reside in the root as endophytes, or directly at the surface of the root, called the rhizoplane, or live in the rhizosphere (Estermann & McLaren, 1961; McNear, 2013). The rhizosphere is the immediate surroundings of the root, and the soil habitat with the highest density of microbes. The plant facilitates this accumulation of microbes by exuding up to 40% of their carbon fixed by photosynthesis into the rhizosphere in order to actively shape their root microbiome (Badri, 2009; Canarini, Kaiser, Merchant, Richter, & Wanek, 2019). This phenomenon is called rhizodeposition. The microbial composition of the rhizosphere is distinct from the microbial composition of the surrounding soil and is characterised by an enrichment of proteobacteria (Figure 2) (Bulgarelli et al., 2012; Edwards et al., 2015; Lundberg et al., 2012). The microbiome of the endosphere is even more tightly controlled by the plant and has a significantly lower diversity and cell density than the surrounding environment (Bulgarelli, Schlaeppi, Spaepen, Themaat, & Schulze-Lefert, 2013). Beneficial microbial consortia can help to fend off pathogenic bacteria, either directly by exuding antimicrobial

molecules, or by competition for the same nutrients, or by enhancing the plants immune fitness, as described below (see 1.7 Plant Immunity). The plant can even actively recruit rhizospheric microbes after a pathogenic attack to stimulate the plant's innate immune system and to fend of pathogens. This phenomenon is termed "cry-for-help", and the released exudates include tryptophan, long-chain fatty acids, coumarins and malate (Peter A. H. M. Bakker, Pieterse, de Jonge, & Berendsen, 2018; Yunpeng Liu et al., 2016; T. Rudrappa, Czymmek, Paré, & Bais, 2008; Stringlis et al., 2018; T. Wen, Zhao, Yuan, Kowalchuk, & Shen, 2021).

A eubiotic (i.e. balanced and healthy) microbiome does not only grant advantages in the struggle with pathogens, but facilitates the plant's overall fitness. Certain microbes help fixing nitrogen, a task the plant is not capable of (B. Singh & Nehra, 2011; Zahran, 1999). Other beneficial microbes promote lateral root growth and the growth of root hairs to consequently increase water and micronutrient intake of plants (Contesto et al., 2010; Qian Li et al., 2022; C. Zamioudis, Mastranesti, Dhonukshe, Blilou, & Pieterse, 2013). Micronutrient acquisition can additionally be enhanced by bacteria or fungi enhancing solubility of phosphate, potassium and iron among others. This is achieved by changing the pH of the surrounding soil, exuding siderophores or other

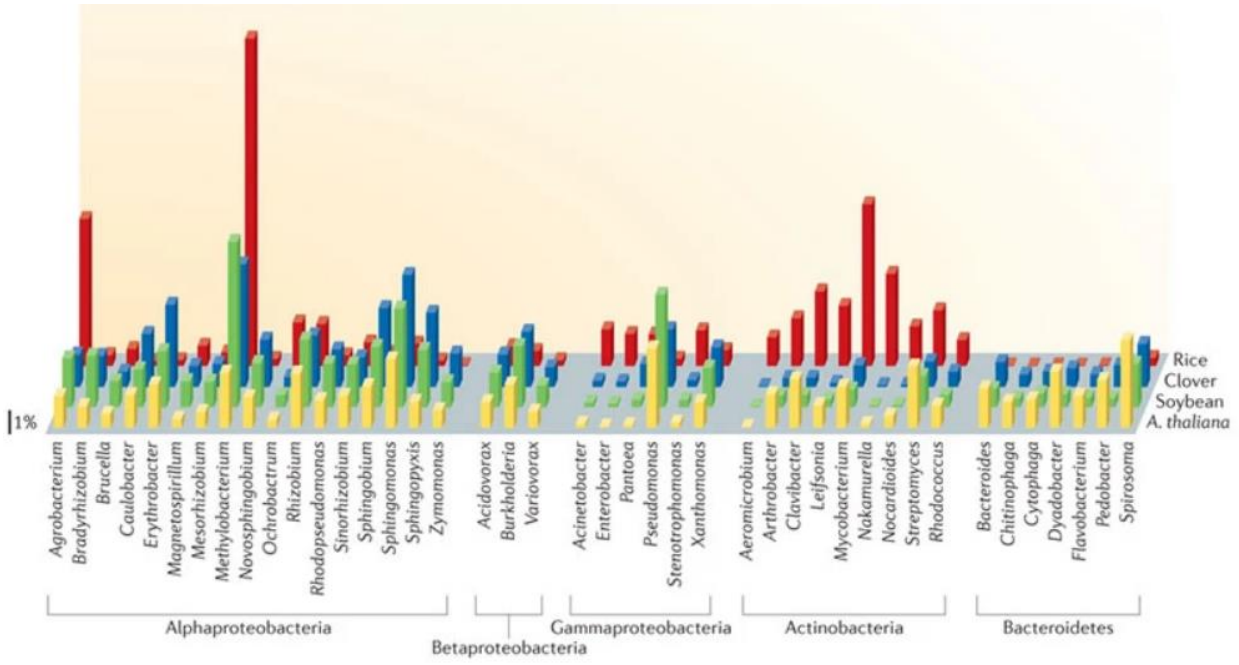

Figure 2: Important bacterial genera in different host plants.

Proteobacteria are the most common bacteria found in plants, together with Actinobacteria and Bacteroidetes. Adapted from Vorholt, 2012

substances in the environment to enhance solubility of minerals (Trivedi, Leach, Tringe, Sa, & Singh, 2020).

1.4 MICROBIOME OF THE PHYLLOSPHERE

The microbiome in and on leaves is subject to several more stressors than the rhizospheric microbiome. The availability of water is usually momentary and if it is supplied via rain, it poses the risk of physically dislocating the microorganisms living on the leaves. Further, UV radiation is a serious threat to DNA integrity and cell functioning. Nutrients are scarce, the temperature can widely vary within a short time and the overall habitat is often short-lived, since most perennial plants shed their leaves during winter in temperate latitudes (Julia A. Vorholt, 2012).

To adapt to a harsh leaf environment, microbes display a specific spatial distribution on the leaf surface, e.g. following leaf veins and surrounding stomata. The bacteria also tend to form aggregates and biofilms to prevent desiccation of the cells (Lindow & Leveau, 2002). These aggregates are usually communities of several microbial species and form clusters of around 1000 cells and more (J. M. Monier & Lindow, 2004). The size of these communities positively correlates with water availability. An additional adaption to protect the microbes from UV radiation is the production of pigments and antioxidant enzymes by the bacteria (J.-M. Monier & Lindow, 2003; Remus-Emsermann, Tecon, Kowalchuk, & Leveau, 2012; Sohrabi, Paasch, Liber, & He, 2023).

One important carbon source in the phyllosphere is methanol, a by-product of cell-wall metabolism, which leads to specialised bacteria and fungi dwelling in the phyllosphere microbiome with an enrichment of genes necessary for a methylotrophic lifestyle (Delmotte et al., 2009; Kawaguchi, Yurimoto, Oku, & Sakai, 2011; Sy, Timmers, Knief, & Vorholt, 2005). In general, a variety of different methods to acquire nutrients can be found in the genome of phyllosphere inhabitants. Examples include ATP-binding cassette transporters (ABC-transporters) involved in the uptake of mono- and di-saccharides, enzymes to help with the uptake of various organic acids, sugars and amino acids, TonB dependent transporters to take up siderophores, as well as bacteriorhodopsins to synthesize energy out of light through photosynthesis (Julia A. Vorholt, 2012).

1.5 PLANT IMMUNITY AND PHYLLOSPHERE MICROBIOME COMPOSITION

Several studies have shown that deficiencies in the plant's innate immune system lead to dysbiosis in the microbiome, which eventually produces signs of illness in the plant. Dysbiosis means that the microbial composition is dysfunctional, often accompanied by an overgrowth of a few bacterial strains and thus negatively impacting the health of the host. Chen *et al.* were able to show that an Arabidopsis quadruple mutant (*min7, fls2, efr, cerk1*), deficient in Microbe-associated molecular pattern (MAMP) signaling (see 1.2.1 Local immunity), harboured a microbiome distinct from that of wildtype Arabidopsis and showed lesions on the leaves. If the dysfunctional microbiome of the Arabidopsis mutants was transferred onto the leaves of gnotobiotic wildtype Arabidopsis plants, they, too, showed lesions on the leaves and general symptoms of illness (T. Chen et al., 2020). Further, Pfeilmeier *et al.* showed that RESPIRATORY BURST OXIDASE HOMOLOGUE D (RBOHD) (which is necessary for the induction of the ROS burst in pathogen-triggered immunity (PTI) and effector triggered immunity (ETI)) is required for the formation of a healthy microbiome on the phyllosphere (Pfeilmeier et al., 2021). Finally, Vogel *et al.* showed that in Arabidopsis mutants lacking the PTI receptors BRASSINOSTEROID INSENTITIVE 1 ASSOCIATED RECEPTOR KINASE 1 (BAK1) and BAK1-LIKE (BKK1), bacteria which have been proven to be beneficial in Arabidopsis wild-type plants can change their role and turn to a pathogenic lifestyle on the plant (C. M. Vogel, Potthoff, Schäfer, Barandun, & Vorholt, 2021).

1.6 CHALLENGES IN THE STUDY OF THE MICROBIOME

The study of the plant's microbiome is faced with many challenges, most of them founded in the complexity of the system. One single bacterial species by itself can change its metabolism and behaviour depending on the cell density in the surrounding environment. This is achieved by chemical-based communication, so-called "quorum

sensing” (Abisado, Benomar, Klaus, Dandekar, & Chandler, 2018). On the other hand, two different bacteria combined can behave quite differently when compared to the one bacterium alone. This is facilitated by changes in the metabolism caused by microbe-microbe interactions (Scherlach & Hertweck, 2018). Considering the interaction of the microbe(s) with the plant, the behaviour can once more change altogether (Lidbury et al., 2022; C. M. Vogel et al., 2021). This makes it almost impossible to predict the outcome of the behaviour of a single bacterial species in a complex microbial community if it was characterized beforehand as a single organism. Great improvements have been made in this regard by the Vorholt group and Schulze-Lefert group by establishing bacterial cultures of over 400 bacterial strains found in the phyllosphere (*At*-LSPHERE) and rhizosphere (*At*-RSPHERE) of wild-living Arabidopsis plants collected in Germany and Switzerland (Bai et al., 2015; Wippel et al., 2021). In addition to the bacterial cultures, full genome sequences are known for all these bacteria, which is a very helpful in characterising functional traits of microbiome communities. This and other culture collections are a huge asset in studying microbiome through SynComs (Bai et al., 2015; J. A. Vorholt, Vogel, Carlstrom, & Muller, 2017; Wippel et al., 2021). However, in this context, it is noteworthy that only a fraction of the bacteria residing in and upon plants are actually culturable in the lab at this time. Numbers range from < 10 % (Heribert Hirt, personal communication) to c.a. 70% (Sarhan et al., 2019). This means that mainly genetic methods are used to provide an overview of the complete microbiome of the plant. This is currently mostly achieved by RT-qPCR if the presence of single known bacteria strains is to be monitored (for example in food quality control) (Postollec, Falentin, Pavan, Combrisson, & Sohier, 2011). Amplicon sequencing of the 16S rDNA is often used to give a general idea of the microbial composition. For this method, a section of the DNA coding for the small subunit of the ribosome is amplified via PCR and then the amplicons are sequenced. The 16S rDNA has conserved regions which are very well suited as primer-binding site since it allows the use of universal primers for a very wide range of bacterial groups (D’Amore et al., 2016). The genetic sequence, between these conserved regions contains highly variable regions which allow for phylogenetic assignment of the sequences (Fricker, Podlesny, & Fricke, 2019). The limiting factor of this method is the amplicon read length of Illumina sequencing systems (the by far most often used sequencing system for this research question) which is about 300 base pairs (bp) per read on the MiSeq system. With paired end reading, meaning

sequencing from both sides of the PCR product and then merging the reads in silico, the maximum PCR product length is around 400-500 bp (T. Hu, Chitnis, Monos, & Dinh, 2021). This does not allow for a discriminating resolution of phylogenetic affiliations of the bacteria found in the sample (Ranjan, Rani, Metwally, McGee, & Perkins, 2016). Exemplary for this phenomenon, the genus *Bacillus* may be named. It is not possible to discriminate between the highly pathogenic *B. cereus,* which can lead to severe infections in humans, and the PGPR *B. thuringiensis*, which has been used in this study, just by sequencing the aforementioned region of the 16S rDNA of the bacteria (M. L. Chen & Tsen, 2002). This illustrates the hindrances met by using amplicon sequencing for studying plant microbiomes. Third generation sequencing technologies (for example Oxford NanoPore Technologies or PacBio) are becoming available, which allow for much longer sequence reads and thus help to overcome these limitations. They often suffer, however, from higher error rates and are much more expensive than Miseq based Amplicon sequencing (Cui et al., 2020). Then again, PacBio presented a new HiFi methodology in 2019 for reads of at least 2kb range and an accuracy of >99,9%. This may be a promising new way of studying microbiomes in plants (Wenger et al., 2019).

An alternative to the amplicon sequencing is the so-called shotgun-sequencing. In this method, all the DNA or RNA present in a sample is amplified with universal short primers, sequenced, and then this whole collection of short sequences is aligned into bigger contigs using high performance computing. This can be accomplished with the short read length of an Illumina system (Ranjan et al., 2016). However, this method is only applicable for microbes living on the surface of plants (e.g., leaves and roots), which can be washed off. Consecutively, the PCR can be performed on the bacteria in the wash medium. Endophytes can only be targeted if the whole plant is used for DNA isolation and PCR. In this case, the plant material by far surmounts the bacterial genetic material, and thus, hardly a conclusive picture emerges (Nobori et al., 2018). However, especially endophytes, which live in close contact and interaction with the plant, are often of special interest. To mitigate this problem, host-specific CRISPR/Cas9 gRNAs have been developed for rice to reduce the amount of plastid DNA in microbiome samples from the endosphere (L. Song & Xie, 2020).

A last challenge in studying microbial communities is the variety of organisms they comprise. The best studied group of organisms in microbiomes are bacteria, followed by fungi. Archaea, viruses and other eukaryotic unicellular organisms such as

oomycetes and algae are strongly neglected (Hassani et al., 2018; Laforest-Lapointe & Whitaker, 2019) . Thus, a big part of the picture has yet to emerge in microbiome studies.

1.7 Plant Immunity

1.7.1 Local immunity

Pathogen-triggered immunity (PTI) is the very first line of plant defence against pathogens beyond the physical barriers including the cuticle and cell wall (Somerville et al., 2004; Yeats & Rose, 2013; Yuan, Ngou, Ding, & Xin, 2021). Usually, PTI is sufficient to fend off adapted pathogens. To this end, the so-called pattern-recognition receptors (PRRs) are located on the cell-surface to detect the presence of pathogen associated molecular patterns (PAMPs) (Jones & Dangl, 2006). PAMPs are also termed microbe associated molecular pathogens (MAMPS), since not every microbe releasing these molecules is necessarily a pathogen. Those MAMPS include flg22 (a fragment of bacterial flagellin), chitin and lipopolysaccharide Lipid A, among many others (Gómez-Gómez & Boller, 2000; Ranf et al., 2015; J. Wan, Zhang, & Stacey, 2004). The PRR-receptor FLAGELLIN SENSITIVE 2 (FLS2), for example, recognises flg22, and upon binding, interacts with downstream receptor kinases including BAK1 and BIK. Thus a phosphorylation-cascade is set into motion (Chinchilla et al., 2007; Gómez-Gómez & Boller, 2000; Heese et al., 2007; D. Lu et al., 2010; Nailou Zhang, Zhou, Yang, & Fan, 2020). This leads to a rapid Ca^{2+} influx into the cytosol within seconds to minutes after detection of MAMPs. Shortly after, a burst of reactive oxygen species (ROS), mediated by RBOHD, is activated. Eventually, the phosphorylation cascade which includes Mitogen-activated protein kinase (MPK)3, MPK4 and MPK6 leads to transcriptional changes in the cell, for example by phosphorylation of TFs such as WRKY33 (Andreasson et al., 2005; Kadota et al., 2014; Y. Liu & Zhang, 2004; Mao et al., 2011; Scheel, 1998). This leads to enhanced camalexin synthesis (Qiu et al., 2008), expression of PAHTOGENESIS-RELATED 1 (*PR1)* (Djamei, Pitzschke, Nakagami, Rajh, & Hirt, 2007) and *PLANT DEFENSIN 1.2* (*PDF1.2)* gene expression via ERF transcription factors (Meng et al., 2013). This is the very first line of defence

upon extracellular encounter of microbial molecules and can start within minutes of the encountering event (Nakano & Shimasaki, 2024).

Some pathogens, however, have evolved to overcome the PTI response. They secrete so-called effectors into the plant cell in order to disrupt the PTI signaling cascade and thus evade the defence response of the plant. In a constant arms race, plants have developed sentinel proteins to counteract the effector triggered susceptibility (ETS). This mechanism is termed the “guard hypothesis”. These intracellular sentinel proteins, namely Nucleotide-binding–Leucine-rich repeat protein (NLR) detect either the effectors directly or indirectly by detecting a “pathogen-induced modified self” (Dangl & Jones, 2001; Jones & Dangl, 2006). Detection of effectors by NLRs leads to a strong defence response in the plant, so-called effector-triggered immunity (ETI), facilitated by ROS-burst, Ca^{2+} influx, activation of phosphorylation cascades and other mechanisms (Grant et al., 2000; Levine, Tenhaken, Dixon, & Lamb, 1994; J. Su et al., 2018; Tsuda et al., 2013). In the case of ETI this often leads to programmed cell death in the so-called hypersensitive response (HR) in order to impede the proliferation of (hemi-) biotrophic pathogens (Balint-Kurti, 2019; Greenberg & Yao, 2004; Jones & Dangl, 2006; Tao et al., 2003). ETI appears stronger than PTI although similar processes underly both responses. Both, PTI as well as ETI, induce a fast and short-lasting ROS burst. Induction of ETI leads to a second, comparatively longer lasting, intensive ROS-burst, at least in part facilitated by RBOHD (Ngou, Ahn, Ding, & Jones, 2021; Yuan, Jiang, et al., 2021). The Ca^{2+} influx following ETI is slower but longer-lasting than PRR-triggered CA^{2+} influx (Grant et al., 2000). A similar pattern can be observed with regard to MAPK activation: NLR-induced MAPK activation is slower but longer-lasting than PRR-induced MAPK activation (J. Su et al., 2018; Tsuda et al., 2013).

PTI and ETI were long thought to be separate immune mechanisms independent of each other. Ngou *et al.* (2021) as well as Yuan *et al.* (2021), however, were able to show that both responses are tightly intertwined and fortify each other (Figure 3). For example, PRRs are a prerequisite for successful triggering of ETI, whereas ETI activation will upregulate PRR levels. Additionally, PRRs are essential for RBOHD phosphorylation, whereas NLR activation leads to enhanced levels of RBOHD in the cells. Those are just two examples of convergence and mutual fortification of PTI and ETI signaling. A lot of elements are not fully understood yet, the interaction in activation

of the MAPK cascade being one of those (Ngou et al., 2021; Yuan, Jiang, et al., 2021; Yuan, Ngou, et al., 2021).

The triggering of ETI can prompt a systemic immune response to elicit heightened immunity in the whole plant. This heightened immunity is called systemic acquired resistance, or, in short, SAR, which is described in more detail below. The current state of knowledge with regard to local immunity is extensively reviewed by (El Kasmi, 2021) and (Nabi et al., 2024; X.-Q. Yu et al., 2024; Yuan, Ngou, et al., 2021)

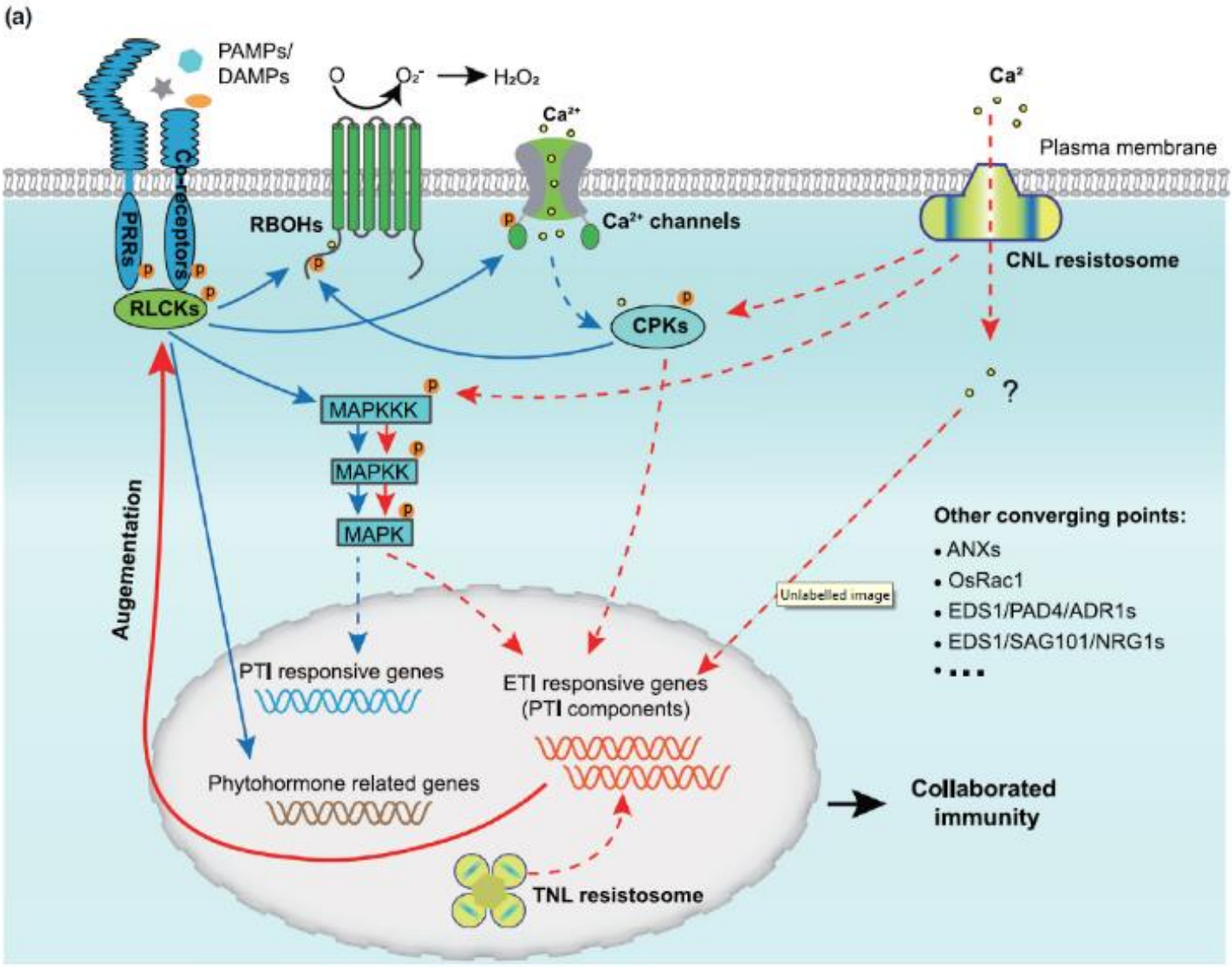

Figure 3: PRR and NLR signaling leading to PTI and ETI.

If PAMPs are recognized, membrane-localized PRRs facilitate phosphorylation of downstream elements, leading to a ROS-burst, Ca^{2+} influx and transcript accumulation of defence-related genes. Adapted from Yuan et al. 2021

1.7.2 Phytohormones involved in plant immunity

Phytohormones are a central element of plant communication and essential for adaptation to changing and possible adverse environmental situations. They are often functional even at very low concentrations and the message relayed can be highly dependent on the concentration of the phytohormone as well as the context: Some phytohormones have different effects depending on temperature, time of day or in their interaction with other phytohormones (Aerts, Pereira Mendes, & Van Wees, 2021; Griebel & Zeier, 2008; Huot et al., 2017). This broadens the width of possible responses of plants to a changing environment.

The phytohormones that are associated with plant immunity include jasmonic acid (JA), salicylic acid (SA) and ethylene (ET). The phytohormone abscisic acid (ABA) is mainly associated with plant responses to abiotic stress. However, it has also been proposed to play an important role in plant defence against pathogens (C. W. Lim, Baek, Jung, Kim, & Lee, 2015).

In addition, one important signaling compound will be described in more depth. This molecule, pipecolic acid (Pip), is not by definition a plant hormone, but still essential for signaling in plant defence reactions.

Since these phytohormones are essential in communicating systemic resistance throughout the whole plant, it seems prudent to discuss the specifics of immunity-related phytohormones at this point before transitioning from the local resistance towards the mechanisms underlying different types of systemic resistances.

JASMONIC ACID (JA)

JA plays a vital role in the defence against necrotrophic pathogens and chewing insects (Aerts et al., 2021; Claus Wasternack, 2015). Besides its role in defence against biotrophic stress, it is also important for flower development, leaf senescence, and root formation (Huang, Liu, Liu, & Song, 2017; Lakehal & Bellini, 2019).

JA biosynthesis starts in the chloroplast from galactolipids, which are formed into the JA precursor 12-oxophytodienoic acid (OPDA). One step in this transformation involves 13-lipoxygenases (13-LOX). The coding genes for these enzymes are

important marker genes for JA-biosynthesis. Varying numbers of *13-LOX* genes exist in different plants, for example four in *Arabidopsis* and eight in rice (S. Wan & Xin, 2022). Once the precursor 12-oxophytodienoic acid (OPDA) is formed, it can be imported into the cytosol, where it functions as a signaling molecule by itself. Then, it is further processed in the peroxisome to JA and exported subsequently into the cytosol (C. Wasternack & Song, 2017).

Jasmonic acid is converted into an abundance of derivatives subsumed under the term jasmonates. Those include the biologically active form (3*R*,7*S*)-JA-L-Ile and the volatile organic compound methyl jasmonate (MeJA) (Fonseca et al., 2009; Pauwels et al., 2008). In the cytosol, JA is conjugated to JA-isoleucin (JA-Ile) by JASMONATE RESISTANT 1(JAR1) (Staswick & Tiryaki, 2004; Suza & Staswick, 2008). The transport of Ja-Ile into the nucleus is facilitated by an ABC-G-transporter JAT1 (Q. Li et al., 2017). In the absence of corresponding stress, the JA levels in the cells are low and the transcription of JA-induced transcription factors like MYC2 and EINs is blocked by JASMONATE-ZIM-DOMAIN PROTEIN 1 (JAZ) proteins. JAZ proteins interact with the co-repressors TOPLESS and NINJA to silence JA dependent signaling (Pauwels et al., 2010). If the nuclear levels of JA-Ile rise, JA binds to the CORONATINE INSENSITIVE 1 (COI1) component of the a SKP1–CUL1–F-box protein (SCF) E3 ubiquitin ligase complex (SCF^{COI1}), which in turn binds to JAZ-proteins to facilitate their ubiquitination and ultimately their degradation (Ali & Baek, 2020; Chini et al., 2007; Sheard et al., 2010; Thines et al., 2007; Xie, Feys, James, Nieto-Rostro, & Turner, 1998). Once the JAZ proteins are degraded TPL and NINJA also dislocate from JA target genes. MYC2 and other TFs are now derepressed and JA dependent gene expression can ensue (Chini et al., 2007; Thines et al., 2007; Yan et al., 2007).

JA signaling is proposed to be divided into two antagonistic pathways (Figure 4) (C. M. Pieterse, Van der Does, Zamioudis, Leon-Reyes, & Van Wees, 2012). The first of them is the ERF branch, which is additionally regulated by ET and is effective against necrotrophic pathogens, especially necrotrophic fungi. The main transcription factors of this branch are ETHYLENE-INSENSITIVE3 (EIN3), EIN-LIKE 3 (EIL3) and their downstream transcription factor ETHYLENE REPONSIVE ELEMENT BINDING FACOTR (ERF), as well as OCTADECANOID-RESPONSIVE ARABIDOPSIS 59 (ORA59) (K. N. Chang et al., 2013; Z. Zhu, 2014). On the other hand, the MYC branch is co-regulated by abscisic acid (ABA) and is active in the defence against chewing insects and wounding (H. Liu & Timko, 2021). The ABA receptor PYR1-LIKE 6 (Pyl6)

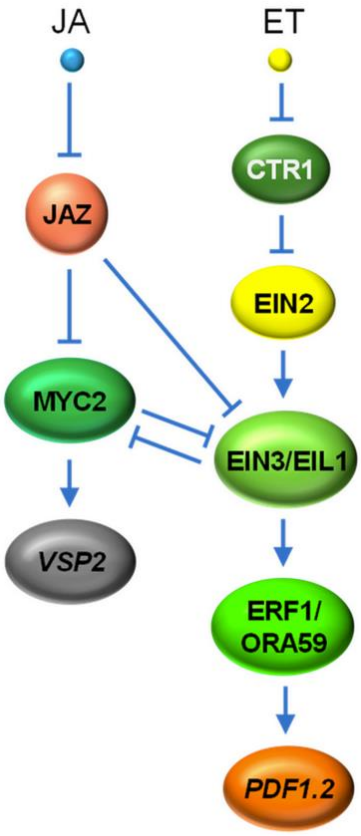

Figure 4: Overview over essential components and interactions in the JA/ET signaling pathways.

Heightened levels of bioactive JA-Ile lead to degradation of JAZ proteins and thus activation of MYC2 dependent gene expression as well as ET dependent gene expression. MYC2 represses ET dependent signaling by interaction with TFs EIN3 and EIL1 and thus repressing JA/ET dependent TFs such as ERF1 and ORA59, which again represses downstream gene expression. Adapted from Liu & Timko 2021

interacts with the JA transcription factor (TF) MYC2 and thus changes gene expression to favour the MYC signaling pathway (Aleman et al., 2016). MYC2 can bind to EIN3 and repress its TF activity while EIN3 and EIL3 can conversely repress MYC2 activity by binding to it. *JASMONATE INSENSITIVE 1 (jin)1* is the gene encoding for MYC2 and thus being used for monitoring MYC2 dependent signaling (S. Song et al., 2014; X. Zhang et al., 2014). VSP1 is a vegetative storage protein, which is upregulated upon JA signaling and thus is used as an JA signaling marker gene (Guerineau, Benjdia, & Zhou, 2003)

JA as well as the volatile MeJA are mobile jasmonates and thus able to reach the whole plant via the phloem to confer resistance against biotic and abiotic stresses (Thorpe, Ferrieri, Herth, & Ferrieri, 2007; Y. Wang, Mostafa, Zeng, & Jin, 2021).

SALICYLIC ACID (SA)

Salicylic acid has been well known and used by humanity as an analgesic long before its importance in plant signaling was discovered. Even Neanderthals were found to having chewed poplar rich in SA to ameliorate tooth ache (Weyrich et al., 2017). Today,

this phytohormone is mainly associated with plant defence against (hemi-) biotrophic pathogens, but is also known to play a vital role in other plant processes such as thermogenesis and flowering (Cleland, 1974; Cleland & Ajami, 1974; Raskin, Turner, & Melander, 1989; C. Vlot, Dempsey, & Klessig, 2009). The first proof for SA involvement in defence was found 1979 in tobacco (White, 1979). Since then, tremendous progress has been made in understanding the synthesis, regulation, and function of SA. In plants, there are two distinct pathways to synthesize SA from the educt chorismate. In Brassicacean plant defence, SA is mainly produced via the isochorismate synthase (ICS) pathway (Mary C Wildermuth, Julia Dewdney, Gang Wu, & Frederick M Ausubel, 2001). The second pathway for SA synthesis is via the phenylalanine ammonia lyase (PAL), which is equally important as the ICS pathway in pathogen defence for plants like tobacco or rice (He et al., 2020; Ogawa et al., 2006; Shine et al., 2016). The amount of bio-active SA in the cell is tightly regulated. This is, on the one hand, achieved by controlling the SA synthesis rate. On the other hand, this is also attained by converting SA into a plethora of derivates, which are not biologically active. Among them are 2,5-dihydroxybenzoic acid, SA 2-*O*-β-D-glucose (SAG) or methyl-SA (MeSA), a plant volatile important in systemic signaling (Noutoshi et al., 2012; Schweizer et al., 1997; Seskar, Shulaev, & Raskin, 1998; Wenig et al., 2019; Y. Zhang et al., 2017).

The most extensively researched SA receptor in plant defence is by far the NON-EXPRESSOR OF PR1 (NPR1) protein (Manohar et al., 2014; Noutoshi et al., 2012; Y. Wu et al., 2012). In the absence of SA, it is located in the cytosol as oligomers. Upon contact with SA and through changes in the cellular redox status, facilitated by SA, it disintegrates into monomers. (Mou, Fan, & Dong, 2003; Tada et al., 2008). This enables relocation to the nucleus where it confers resistance through several transcription factors, including TGA2, TGA5, and TGA6 (H. S. Kim & Delaney, 2002; Mahdi et al., 2021; Nguyen et al., 2022; L. Sun et al., 2022; Yuelin Zhang, Fan, Kinkema, Li, & Dong, 1999; Yuelin Zhang, Tessaro, Lassner, & Li, 2003). The NPR1-like receptor proteins NPR3 and NPR4 are highly similar in their structure to NPR1, despite conversely functioning in the suppression of SA associated gene expression if SA-levels in the cytosol are low (Ding et al., 2018; Yuelin Zhang et al., 2006). SA-mediated signaling and transcription changes are essential for local immunity in the form of PTI and ETI as well as systemic resistance, in the form of SAR and some forms of IR. Upon SA signaling, PR1 is upregulated in an NPR1 dependent manner and thus

is used to detect SA dependent signaling in a very reliable manner. Noteworthy enough, the function of PR1 in Arabidopsis is not yet elucidated (Laird, Armengaud, Giuntini, Laval, & Milner, 2004). Comprehensive reviews were written among others by Klessig et al, Peng et al, and Vlot *et al.* (Klessig, Choi, & Dempsey, 2018; Peng, Yang, Li, & Zhang, 2021; C. Vlot et al., 2009).

ABSCISIC ACID (ABA)

Abscisic acid is mainly known to be involved in the response to abiotic stress such as drought and high salinity as well as in the regulation of developmental processes such as seed dormancy and leaf senescence (K. Chen et al., 2020). ABA is synthesized out of C_{40} β-carotenes in plastids and after several processing steps, the precursor xanthoxin is transported into the cytosol and further processed into ABA (Arc, Sechet, Corbineau, Rajjou, & Marion-Poll, 2013; Nambara & Marion-Poll, 2005). If no active ABA signaling is taking place in the plant cells, there are only basal levels of ABA in the cytosol. This is important for normal growth and development of the plant (K. Chen et al., 2020). The bulk amount of ABA is stored in the endoplasmic reticulum and the vacuole in the biologically inactive form of ABA-glucose ester (ABA-GE) (Z. Liu et al., 2015; Ma et al., 2018). Upon the encounter of stress, the ABA-GE is rapidly transformed into ABA and transported into the cytosol. Thus, a very fast adaption to unfavourable circumstances is possible (Lee et al., 2006; Ma et al., 2018; Xu et al., 2012). In addition, ABA can be transported from the leaves, where it is mainly synthesized, into the shoot and roots via active ABA transporters, e.g., transporters of the ABC-G family (Kang et al., 2011; Kuromori et al., 2010; F.-P. Zhang et al., 2018). ABA is not only involved in abiotic stress response, but also in defence against pathogens. The best-known example is the involvement of ABA in the closure of stomata, which is important for water conservation in time of drought, but also hinders the entrance of pathogens (Guzel Deger et al., 2015; Jianbin Su et al., 2017). During plant defence against pathogens, ABA is considered to play an ambivalent role. On the one hand, ABA deters pathogen entrance by the closure of stomata in a SA dependent manner. On the other hand, however, it hinders resistance at later infection phases, for example by repressing callose deposition after pathogenic challenge (de Torres-Zabala et al., 2007). Additionally, it infers with plant immunity by impeding plant systemic responses for example by antagonising SA signaling or blocking the JA-ERF-

pathway by interaction with the ABA receptor PYL6. (Aleman et al., 2016; Mohr & Cahill, 2007; Ton, Flors, & Mauch-Mani, 2009; Yasuda et al., 2008). A typical marker gene for the ABA-co-regulated JA signaling pathway would be *VSP2* and for ABA signaling alone would be *LEA4* (Papadopoulou, Maedicke, Grosser, van Dam, & Martínez-Medina, 2018).

Ethylene (ET)

Ethylene is one of the plant hormones involved in defence against plant pathogens. It is a gaseous phytohormone involved in many plant developmental processes including fruit ripening, seed germination, senescence, and abscission. In addition, it is involved in the response to abiotic as well as biotic stresses (Binder, 2020). ET is synthesized out of the amino acid methionine in several steps, including conversion to *S*-adenosyl-methionine, 5′-methylthioadenosine and finally the direct ET precursor 1-aminocyclopropane-1-carboxylic acid (ACC) (Broekaert, Delauré, Bolle, & Cammue, 2006; Fontecave, Atta, & Mulliez, 2004; Kende, 1993). For Arabidopsis, five ET receptors are known, namely ETR1, ERS1, ETR2, ERS2, and EIN4, which are all located in the membrane of the endoplasmic reticulum (Ju & Chang, 2015). Those receptors supress ET signaling in the absence of ET via the protein kinase CTR1 (Kieber, Rothenberg, Roman, Feldmann, & Ecker, 1993). Upon perception of ET, the repression is lifted, and EIN2, a positive regulator of ET signaling can activate the transcription factors EIN3 and its homolog EIL1 at the nucleus (Alonso, Hirayama, Roman, Nourizadeh, & Ecker, 1999; An et al., 2010; Chao et al., 1997; Ju et al., 2012; Qiao et al., 2012; X. Wen et al., 2012). These transcription factors then are able to start signaling cascades, often while integrating additional signaling cues by other phytohormones (Katherine Noelani Chang et al., 2013; Ju & Chang, 2015). This holds especially true for the interaction of JA and ET. EIN3/EIL1 are pivotal in the activation of the so-called ERF pathway to fend of pathogenic fungi. This pathway is repressed by the JA-dependent MYC2-pathway (see “JA”), and expresses, once activated, defence-related genes such as *ERF1, ORA59*, and *PDF1.2* (X. Dong, 1998; Oscar Lorenzo, Chico, Sánchez-Serrano, & Solano, 2004; O. Lorenzo, Piqueras, Sánchez-Serrano, & Solano, 2003; Z. Zhu et al., 2011)

Pipecolic acid (Pip)

Pipecolic acid is a non-proteinogenic amino acid and not traditionally named among plant hormones. Still, it plays a pivotal role in plant defence signaling against pathogens, especially SAR. It is synthesized out of Lys by AGD2-LIKE DEFENCE PROEIN 1 (ALD1) and SAR-DEFICIENT4 (SARD4) in the chloroplast and converted to its biological active form N-hydroxy pipecolic acid (NHP) by FLAVIN-DEPENDENT MONOOXYGENASE 1 (FMO1) in the cytosol (Michael Hartmann & Zeier, 2018; M. Hartmann et al., 2018; Mishina & Zeier, 2006; Navarova, Bernsdorff, Doring, & Zeier, 2012; J. T. Song, Lu, McDowell, & Greenberg, 2004). For a long time, Pip was thought to act independently and in parallel to SA. However, recent studies suggest that Pip signaling is tightly interwoven with SA signaling, and both are regulated by shared mechanisms. Regulatory elements include the defence proteins EDS1 and PAD4 as well as transcriptional regulators SARD1, CBP60g and NPR1 (Feys, Moisan, Newman, & Parker, 2001; M. Hartmann et al., 2018; T. Sun et al., 2018; T. Sun et al., 2015; C. Vlot et al., 2021; L. Wang et al., 2011; Yildiz et al., 2021). Application of SA can increase NHP production and downstream signaling, and vice versa, NHP application can enhance SA synthesis and signaling (Yildiz et al., 2021).

In local tissue, Pip accumulation is promoted in a positive feedback loop including MPK3/MPK6 and WRKY33 (Y. Wang et al., 2018). In systemic tissue, Pip accumulation is additionally fortified by in a NO/ROS, azelaic azid (AzA) and LEGUME LECTIN-LIKE PROTEIN 1 (LLP1) dependent manner as well as by monoterpene volatile organic compounds (VOCs) (Wenig et al., 2019).

1.7.3 Systemic immunity

Phytohormones allow the triggering of long-distance communication within the plant organism to induce resistance not only at the site of stress perception but systemically in the whole organism.

Some microbes can activate such systemic plant defence mechanisms, including systemic acquired resistance (SAR) and induced systemic resistance (ISR). While SAR is induced in systemic tissues of plants undergoing a local pathogen infection, ISR takes effect in aerial tissues of plants interacting with beneficial microbes in the rhizosphere (A. C. Vlot et al., 2020). This previously clear distinction, however, is blurring evermore as our understanding of the signaling pathways underlying induced resistance expands. In this thesis, I follow the suggestions of De Kesel and colleagues (De Kesel et al.) to use the term Plant Growth Promoting Rhizobacteria/Fungi Induced Resistance (PGPR/F IR) or short IR instead of ISR, since it seems to encompass not only one distinct mechanism (see the subchapter on IR). I will continue to use the term SAR, since this form of plant immunity seems to be distinct and well-defined in the way of elicitation as well as signal transduction.

<u>SAR</u>

If pathogens trigger either PTI or ETI locally, this can lead to a signaling cascade, which spreads in a short time via signaling molecules to the whole plant and elicits a status of heightened immunity in the whole plant (C. Vlot et al., 2021). This heightened immunity, termed SAR, can last from several days up to and including more than one generation (Luna, Bruce, Roberts, Flors, & Ton, 2012). This transgenerational defence is often achieved via priming (for further explanation, please see further down “PGPR IR”), especially via epigenetic changes (U. Conrath, G. J. M. Beckers, C. J. G. Langenbach, & M. R. Jaskiewicz, 2015). The molecular mechanisms of SAR in dicots such as *A. thaliana* are well-characterized. SAR depends on two distinct but interwoven signaling pathways, one depending on salicylic acid (SA), the other on pipecolic acid (Pip) (M. Hartmann & Zeier, 2019; A. C. Vlot et al., 2020).

Locally as well as systemically, a rise of SA levels leads to an enhanced conversion of the biologically active SA to the biologically inactive, but highly mobile MeSA via a SA methyltransferase (SAMT) (F. Chen et al., 2003; P.-P. Liu, Yang, Pichersky, & Klessig, 2010; Park, Kaimoyo, Kumar, Mosher, & Klessig, 2007; Ross, Nam, D'Auria, &

Pichersky, 1999; C. Vlot et al., 2009; Zubieta et al., 2003). The methyl esterase SABP2 hydrolyses MeSA to SA. MeSA and SA form a stable equilibrium until SA levels rise and inhibit SABP2 activity, thus shifting the equilibrium towards enhanced MeSA levels (Forouhar et al., 2005; Kumar & Klessig, 2003; Pokotylo, Kravets, & Ruelland, 2019). MeSA is highly volatile and mobile via the vasculature as well as the air (Park et al., 2007; Shulaev, Silverman, & Raskin, 1997). SA itself is also mobile, albeit at a lower level (L. Chen et al., 2019). After local infection of a pathogen, the SA levels rise, shifting the equilibrium towards MeSA formation. MeSA then moves via air and phloem to systemic tissues where it is converted back to SA and thus induces a systemic defence reaction (G.-H. Lim et al., 2016; Park et al., 2007; C. Vlot et al., 2021).

In addition, pipecolic acid levels as well as the level of the biological active form NHP rise locally upon perception of a suitable SAR trigger (Y. C. Chen et al., 2018). This heightened PIP/NHP synthesis is also stabilised via a self-fortifying feedback loop. This feedback loop is driven by the kinases BAK1/BKK1 as well as the MAP kinases MPK3/MPK6 and the transcription factor WRKY33 (C. Vlot et al., 2021; Y. Wang et al., 2018). Heightened levels of SA and Pip further fortify each other via a SARD1/CBP60g and NPR1 dependent feedback-loop in local infected as well as systemic tissues (T. Sun et al., 2020).

Heightened Pip/NHP levels lead to accumulation of azelaic acid (AzA), triggered by nitric oxide (NO) and reactive oxygen species (ROS) generation (C. Wang et al., 2018). Higher AzA levels again lead to heightened levels of the putative lipid transfer proteins AZELAIC AZID INDUCED (AZI1) / EARLY ARABIDOPSIS ALUMINUM INDUCED 1 (EARLI1), which facilitate AzA symplastic movements (Jung, Tschaplinski, Wang, Glazebrook, & Greenberg, 2009). The phloem mobile metabolites G3P and DIR1 are also of importance in the Pip/NHP triggered and AzA mediated signal towards systemic tissue and depend on functional AZI1 in the plasmodesmata (Kachroo, Liu, Yuan, Kurokawa, & Kachroo, 2022). However, the exact mechanism is not elucidated to this day (Chanda et al., 2011; Jung et al., 2009; G.-H. Lim et al., 2016; Maldonado, Doerner, Dixon, Lamb, & Cameron, 2002). NHP itself is also phloem-mobile (Y. C. Chen et al., 2018). Another phloem-mobile signaling molecule contributing to the SAR signal transduction is dehydroabietinal, which is dependent on *FLOWERING LOCUS D* (*FLD*) (Chaturvedi et al., 2012) (Z. Chowdhury et al., 2020; V. Singh et al., 2013).

Wenig et al. demonstrated the existence of a further feedback regulation via airborne monoterpenes. The release and perception of those volatile compounds are an integral and essential part of functional SAR elicitation (Wenig et al., 2019).

Monoterpenes are terpenes consisting of two isoprene units which may be either linear or contain rings. A lot of essential oils are based on monoterpenes or monoterpenoids like menthol, limonene, camphor, sabinene and others. Those are often emitted by the plant to interact with the environment, for example pollinators, or to repel pests (Loza-Tavera, 1999). In the transmission of the SAR signal to systemic tissues within the plant as well as to neighbouring plants, the monoterpenes camphene as well as α- and β-pinene are utilized. An important precursor in monoterpene synthesis is geranyl diphosphate, which is synthesized in the plant by the enzyme GERANYL(GERANYL)DIPHOSPHATE SYNTHASE (GGPPS12) (Riedlmeier et al., 2017; Tholl & Lee, 2011; G. Wang & Dixon, 2009; Wenig et al., 2019).

Systemically, perception of monoterpenes, putatively connected to LLP1, induce conversion of Pip to NHP and thus start a feedback loop via NO/ROS accumulation, followed by AzA and G3P accumulation (Wenig et al., 2019; K. Yu et al., 2013). Higher SA and NHP levels again fortify each other in a feedback loop via SARD1/CBP60g (T. Sun et al., 2018). SA biosynthesis is fortified by shifting the SAMT/SABP2 mediated MeSA <-> SA equilibrium towards SA (C. Vlot et al., 2021). To monitor establishment of SAR, *PR1* has been established as a molecular marker (Sticher, Mauch-Mani, & Métraux, 1997).

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PGPR/F IR

IR systemic immunity

Besides the pathogen induced SAR, plants have evolved another mechanism to induce a form of systemic resistance in the whole organism. This so-called Induced Resistance (IR) is usually elicited by beneficial, soil-dwelling microorganisms at or in the roots. Those microorganisms can oftentimes not only elicit a state of heightened immunity, but also increase resistance towards different biotic and abiotic stressors and increase plant growth and are thus termed plant growth promoting rhizobacteria/fungi (PGPR/PGPF). The specific protective and growth-promoting properties vary between microbial strains and respective hosts. The root dwelling IR inducing microbes include rhizobacteria such as *Pseudomonas* spp., *Bacillus* spp.,

Streptomyces spp. as well as several species of fungi, including *Serendipita indica* and *Trichoderma* spp. (Aloo, Makumba, & Mbega, 2019; Alsharif, Saad, & Hirt, 2020; Balmer, Planchamp, & Mauch-Mani, 2013; Gill et al., 2016; Mahmood et al., 2016; Newitt, Prudence, Hutchings, & Worsley, 2019; C. M. Pieterse et al., 2014; Ton, Van Pelt, Van Loon, & Pieterse, 2002; Vacheron et al., 2013). However, IR eliciting microbes do not necessarily have to engage at the roots of the plant. Certain beneficial bacterial strains have also been shown to induce IR at the leaves of *A. thaliana* (C. M. Vogel et al., 2021).

To this date, the best studied IR system is that of *Pseudomonas simiae* WCS417r in *Arabiopsis thaliana*. *Pseudomonas simiae* WCS417 was one of the first PGPRs described in the context of IR in 1988 (Lamers, Schippers, & Geels, 1988). Isolated from disease supressing soil, this strain helped to control the take-all disease elicited by the fungus *Gaeumannomyces graminis* (Y.-S. Kwak & Weller, 2013). Since then, it has become a model organism for studying PGPR IR as it can elicit IR in a plethora of plants, including *Arabidopsis thaliana*, eucalyptus trees, banana plants, radish, and wheat, amongst others (Leeman et al., 1995; Nel, Steinberg, Labuschagne, & Viljoen, 2006; C. M. J. Pieterse et al., 2021; Ran, Liu, Wu, van Loon, & Bakker, 2005). During cultivation in the laboratory, WCS417 gained an antibiotic resistance by mutation and thus gained an additional “r” to its name (from *P. simiae* WCS417 to *P. simae* WCS417r) if the nowadays often used strain with rifampicin resistance is meant.

Pieterse and colleagues found that WCS417 IR at the roots of *A. thaliana* is dependent on JA/ET signaling but not on SA signaling, and the concept of counteracting systemic immunities was reinforced: the SA dependent SAR acting against pathogens with a (hemi-)biotrophic lifestyle on the one hand and JA/ET dependent resistance against necrotrophic pathogens on the other hand (Leon-Reyes et al., 2009).

However, recently, researchers were able to show that the phytohormones involved in conveying the IR signal are highly dependent on the specific IR eliciting bacterial strain as well as the lifestyle of the offending pathogen, be it (hemi-) biotrophic or necrotrophic. In the former case, SA could be shown to play an important role in IR establishment (Kojima, Hossain, Kubota, & Hyakumachi, 2013; Martínez-Medina et al., 2013; Nguyen et al., 2020; Nie et al., 2017; van de Mortel et al., 2012; Vos, De Cremer, Cammue, & De Coninck, 2015; L. Wu et al., 2018).

Despite our knowledge of the involvement of the mentioned phytohormones in eliciting IR, the exact mechanisms from microbial perception towards systemic response are

not yet fully understood. In general, IR seems to depend mainly on the priming of plant reactions, at least for aerial tissues. This means that there are no major transcriptional changes in the leaves of the plant directly upon the encounter with an IR-eliciting microbe. Rather, there are subtle changes, often on the epigenetic level to put the plant in a steady state, able to react fast and strong at the time point of a pathogenic attack (Uwe Conrath et al., 2015; Martinez-Medina et al., 2016; Mauch-Mani, Baccelli, Luna, & Flors, 2017; Pozo et al., 2008). This has the benefit of low metabolic costs with simultaneous heightened resistance. On the other hand, studying IR is made much more challenging by this phenomenon, since the immediate changes in gene transcript accumulation upon elicitation of IR are rather scarce.

There is a plethora of microbial molecules which are involved in eliciting IR at the roots of the plants, of which a few choice examples will be named and described here. Several PGPR, for example, induce a PTI-like response in their hosts upon first encounter, since they usually display similar MAMPs as their pathogenic pendants. This first response is often associated with a milder ROS burst in PGPR encounter than in the pathogenic counterparts, however, it has been shown to be of necessity in order to trigger IR (Jacobs et al., 2011). Other microbe-derived molecules to induce IR include quorum-sensing molecules such as AHLs and CDPs, which are utilized by bacteria to confer information about and react to shifting cell densities (Azimi, Klementiev, Whiteley, & Diggle, 2020). Plants are listening in to this communication and thus QS molecules have been shown to elicit IR in tomato, Arabidopsis, *Nicotiana benthamiana,* barley, cucumber and several other plants (Ortiz-Castro & López-Bucio, 2019).

A multitude of VOCs is emitted by bacteria (to this day, around 1000 VOCs are known) and several of them are involved in triggering IR (Audrain, Farag, Ryu, & Ghigo, 2015). Those include for example 2,3-butanediol, acetoin and nitric oxide (NO), which has been shown to induce SAR in plants. NO can also induce JA/ET dependent resistance signaling in plants. Depending on the VOCs emitted, either a SA dependent or JA dependent or a SA and JA dependent immune response is triggered (Mur, Prats, Pierre, Hall, & Hebelstrup, 2013; Wendehenne, Gao, Kachroo, & Kachroo, 2014).

Fe availability in the soil is a major factor in shaping microbial communities in soil and rhizosphere. Well-adapted rhizospheric microbes can release siderophores – iron chelating compounds- into their surroundings to bind Fe-Ions for later uptake by active transport mechanisms (Lemanceau, Expert, Gaymard, Bakker, & Briat, 2009; L. Zhu,

Huang, Lu, & Zhou, 2022). Those siderophores can trigger an IR in certain plants but can also actually enhance iron uptake by the plant (Lugtenberg & Kamilova, 2009; MEZIANE, VAN DER SLUIS, VAN LOON, HÖFTE, & BAKKER, 2005). The iron homeostasis seems to be an angling-point in IR induction, since MYB72 has been shown to play a role in enhancing iron uptake under iron deficient conditions (Christos Zamioudis, Hanson, & Pieterse, 2014). On the other hand, it has been shown to be pivotal in the induction of IR at the roots (Figure 5) (Segarra, Van der Ent, Trillas, & Pieterse, 2009; C. Zamioudis et al., 2015).

Molecular components so far known for their role in SAR induction such as AZI1 and EARLI1 (see “SAR”) have been shown to be required for induction IR by different bacteria, and gene transcription is either induced or primed in roots as well as leaves upon induction of IR in Arabidopsis (Cecchini et al., 2019; Cecchini, Steffes, Schlappi, Gifford, & Greenberg, 2015; Shine, Xiao, Kachroo, & Kachroo, 2019; Timmermann et

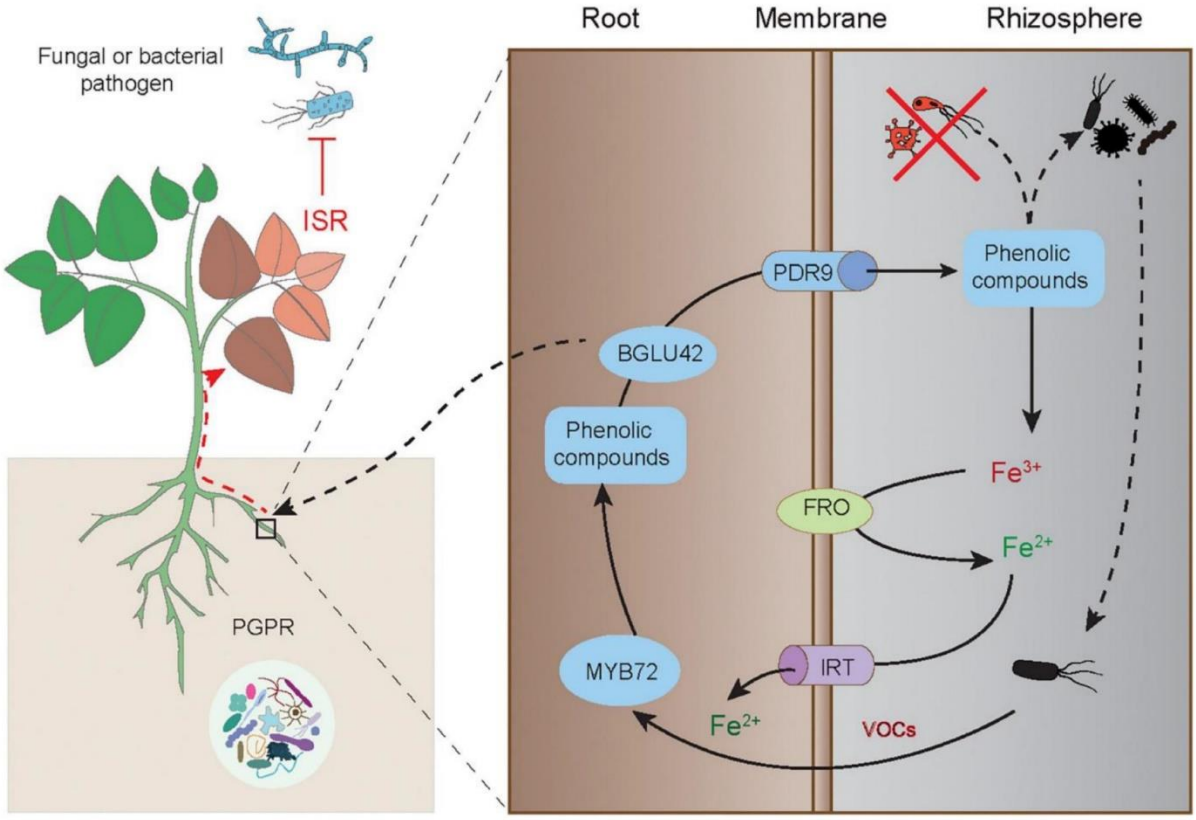


Figure 5: MYB72 is an integral part of the response of plants to some PGPR as well as to iron starvation.

MYB72 gene expression is upregulated upon detection of PGPR released VOCs. MYB72 again activates biosynthesis of phenolic compounds as well as corresponding transporters for those phenolic compounds. Secretion of those molecules promotes solubilization of Fe^{3+} and contributes to compositional changes in the rhizosphere microbiome. Adapted from Zhu et al. 2022.

al., 2019; Christos Zamioudis et al., 2014). Likewise, accumulating G3P in the foliar tissue of soybeans is essential for establishing IR-like responses triggered by rhizobia. NPR1, which has been mentioned before as an integral signaling hub in plant defence, has an SA-independent function in PGPR/F triggered IR. Where SA dependent NPR1 function requires a relocation into the nucleus and oligomer formation, the JA associated function is linked to a localisation of NPR1 in the cytosol (Spoel et al., 2003). The exact signaling mechanism underlying jasmonate signaling during IR is as of yet unclear. On the one hand, there is evidence that JA signaling during IR is dependent on MYC2, which has been shown to be antagonistic toward the ethylene-dependent JA signaling branch (Kazan & Manners, 2013; Pozo, Van Der Ent, Van Loon, & Pieterse, 2008). On the other hand, there is evidence that IR signaling induced by the same bacterium (WCS417r) in the same plant (Arabidopsis) is dependent on ethylene dependent JA signaling conferred by EIN2-7 as well as ETR1 (See ET signaling below) (Knoester, Pieterse, Bol, & Van Loon, 1999; C. M. J. Pieterse et al., 1998) (C. M. Pieterse et al., 2012). How this obvious conundrum resolves *in planta* is not yet understood.

Plants can actively recruit PGPR/F into their rhizosphere to enhance immunity against aboveground pathogens (Figure 6). This is achieved, for example, upon the exudation of coumarins from plant roots into the rhizosphere. Coumarins are secondary metabolites, which are detrimental for a lot of bacteria, whereas specialised rhizobacteria can tolerate them (Stringlis et al., 2018). The attraction of PGPR/F can occur after pathogen attack to help in an acute situation of stress. One example for this is the recruitment of *Xanthomonas sp., Stenotrophomas sp.* and *Microbacterium* sp. to the rhizosphere, after the plant had been infected with the pathogen *Hyaloperonospora arabidopsidis* (R. L. Berendsen et al., 2018). As mentioned before, after activation of SAR, plants can exude various molecules into the rhizosphere to attract beneficial bacteria and alter their transcriptional profile. This can, for example, boost biofilm formation and promote even further immune responses besides the initial SAR response (T. Rudrappa et al., 2008). This does not solely aid the plant in immediate distress. Rather, the beneficial bacteria accumulate in the soil surrounding the plant and can persist there even over longer periods of time after the plant has been removed. Thus, it can promote the health of subsequent generations of the plant

fighting of biotic or even abiotic stresses (Peter A. H. M. Bakker et al., 2018; Roeland L. Berendsen et al., 2018).

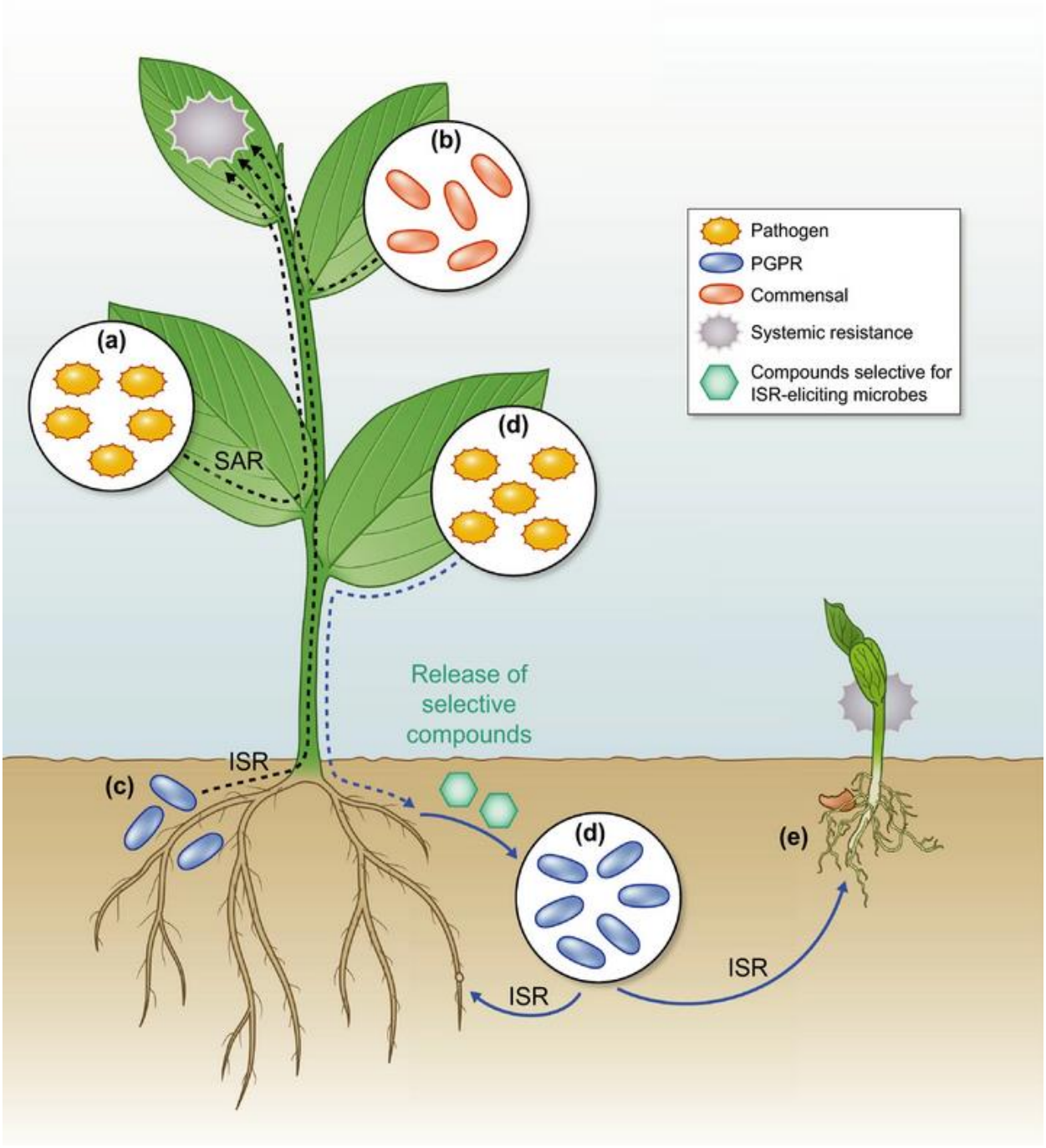


Figure 6: Systemic immunity in plants and interaction with microbes.

Pathogenic bacteria infecting foliar tissues (a) elicit systemic resistance in the form of SAR. Beneficial microbe on the leaves (b) or at the roots (c) can elicit systemic immunity often called IR. If pathogenic bacteria infect foliar tissue, plants can attract beneficial microbes to the rhizosphere to enhance their resistance (d). Following generations can benefit from this enrichment of beneficial bacteria in the soil (e). adapted from Vlot et al. 2021

1.8 AIM OF THIS WORK

The aim of this work is to broaden the general knowledge about IR induced by beneficial bacteria in Arabidopsis. To this end, I will study IR elicited by two different bacteria. One IR eliciting strain is the well characterized model-organism, *Pseudomonas simiae* WCS417r (C. M. J. Pieterse et al., 2021). The other microbial strain is *Bacillus thuringiensis*, which is also well known, albeit not for its immunity enhancing capabilities but rather for its insecticidal properties, conferred by crystalized proteins, so called CRY-proteins. Those proteins became known in the context of the development of the so-called BT-plants such as maize, cotton or even spruce which are more resistant against insect feeding (Mazier, Pannetier, Tourneur, Jouanin, & Giband, 1997). Only in the last years has it become apparent that *Bt* additionally possesses plant growth promoting properties. This makes it an optimal target for dual use by diminishing herbivorous insects and at the same time bolstering the plant's immune system. IR eliciting properties of *Bt* have been shown in tomato (Akram, Mahboob, & Javed, 2013)

In addition, I strive to gain insight into the signaling pathways involved in the elicitation of IR in Arabidopsis. To this end, I make use of various mutants which are deficient in different components of defence signaling or phytohormone synthesis and investigate if these mutants are capable of mounting IR.

A major third focal point I want to address is the microbiome of the phyllosphere with regard to the elicitation of IR. It is known that plants which are deficient in certain parts of their immune response, especially ETI and PTI, show drastic changes in their phyllosphere microbiome (T. Chen et al., 2020; Pfeilmeier et al., 2021; C. Vogel, Bodenhausen, Gruissem, & Vorholt, 2016). On the other hand, Vogel et al. were able to show that certain bacteria of the phyllosphere can elicit an immune response in the plants without being pathogenic. Thus, it seems conceivable that the immune system of the plant may have an impact on the phyllosphere microbiome if IR is elicited. Conversely, it may be possible that changes in the microbiome have an impact on the immune status of the plant. I will approach the subject by collecting leaf material from IR-activated plants and performing amplicon sequencing of the V5-V7 region of the 16S rDNA with bacteria-specific primers to gain insight into the microbial composition in the phyllosphere with and without IR treatment.

As a proof of concept, I will utilize one strain found in the amplicon analysis to be enriched in the phyllosphere of plants which have undergone IR treatment for further experiments. This is aimed to close the circle between immunity, elicited at the roots and the phyllosphere microbiome and potential changes there to aid the process of heightening the plant's immunity.

Taken together, the broader goal of this thesis is to contribute to our knowledge of the natural capabilities of plants to defend themselves against pathogens. This may help to reduce the use of pesticides by bolstering the plants' innate ability to resist pests and diseases. Thus, harvests could be secured at a higher level at reduced usage of pesticides. This, on the other hand, would save money and help to preserve the biodiversity of our flora and fauna, while at the same time ensuring a sufficient food production for the people of our world.

2. MATERIAL

Plants

The plants used where *Arabidopsis thaliana* ecotype Col-0 with the mutants *jin1, npr1-1, sid2, ald1, ggpps12*, and *llp1-1*, which have been described previously (Berger, Bell, & Mullet, 1996a; H. H. Breitenbach et al., 2014; Cao, Glazebrook, Clarke, Volko, & Dong, 1997; Riedlmeier et al., 2017; J. T. Song et al., 2004; Wenig et al., 2019; M. C. Wildermuth, J. Dewdney, G. Wu, & F. M. Ausubel, 2001).

Plants were grown in potting soil ("Floradur® B Seed", Floragard GmbH, Oldenburg, Germany) mixed with silica sand (grain size 0,6-1,2mm) at a ratio of 5:1.

Bacterial and fungal strains

Table 1: Bacterial strains used in this work

Species	Strain	Source
Pseudomonas simiae	*WCS417*r	Corné Pieterse
Bacillus thuringiensis		Michael Rothballer
Pseudomonas syringae pathovar tomato (Pst)	DC3000	Heiko Breitenbach
Flavobacterium spp.	Leaf82	*At*-LSPHERE, Prof. Julia Vorholt, ETH Zürich, Schweiz
Microbial community standard of 10 bacterial strains	Listeria monocytogenes - 12%, Pseudomonas aeruginosa - 12%, Bacillus subtilis - 12%, Escherichia coli - 12%, Salmonella enterica - 12%,	Zymobiomics, Zymo Research, California, USA

	Lactobacillus fermentum - 12%, Enterococcus faecalis - 12%, Staphylococcus aureus - 12%, Saccharomyces cerevisiae - 2%, and Cryptococcus neoformans - 2%.	

Kits

Table 2: Kits used in this work

Name	Manufacturer	Use
SensiMix SYBR Low-Rox Kit	Bioline Reagents, London, UK	qPCR
SuperScript II Reverse Transcriptase	Invitrogen/ Thermo Fisher Scientific, Waltham, USA	cDNA synthesis
Nucleospin Gel + PCR clean up Kit	Macherey-Nagel, Düren, Germany	DNA-isolation from agarosegel
QIAquick gel extraction kit	QIAGEN (Hilden, Germany)	DNA-isolation from agarosegel
FastPrep Soil Kit	MPio, Santa Ana, California, USA	DNA-isolation from leaf-tissue
DNF-473-Standard Sensitivity NGS Fragment Analysis Kit	Agilent, Santa Clara, CA, USA	Analysis of amplicon fragments before sequencing
MiSeq Reagent Kit v3 (600-cycle)	Illumina	Sequencing of Amplicons

Chemicals and Enzymes

Table 3: Chemicals and Enzymes used in this work

Name	Manufacturer
SuperScript II reverse transcriptase	Invitrogen/Thermo Fisher Scientific (Waltham, USA)
NEBNext High Fidelity Polymerase	New England Biolabs, Ipswich, MA, USA
Phytoagar	Duchefa (Haarlem, Netherlands)
Tween-20	Calbiochem (San Diego, USA)
Silwet	Lehle Seeds (Texas, USA)
Murashige-Skoog + vitamins	Duchefa (Haarlem, Netherlands)

Antibiotics

Table 4: Antibiotics used in this work

Name	concentration	manufacturer	use
Kanamycin	50 µg/ml	Roth, Germany	Selection of *Pseudomonas syringae pv tomato* (virulent and avirulent strains)
Rifampicin	100 µg/ml	Duchefa Bichemie, Germany	Selection of *Pseudomonas syringae pv tomato* (virulent and avirulent strains) and WCS417

Buffers and Media

Table 5: Buffers and Media used in this work

Buffer/Medium	ingredients	Application
RNA extraction buffer	3.05 g ammonium thiocyanate, 9.44 g guanidinium thiocyanate, 5 ml glycerol, 3.33 ml 3 M sodium acetate pH 5.2, 40 ml H2O, adjust pH to 5.0, 38 ml Roti-Aqua-Phenol	RNA extraction
Mock buffer	10 mM MgCl2	control treatment for infiltration
TAE (Tris-acetate-EDTA) buffer	40 mM Tris, 1 mM EDTA, 0.1% (v/v) glacial acetic acid	gel electrophoresis
NB	8 g Nutrient Broth No. 4 (Fluka Analytical/ Sigma-Aldrich, St. Louis, USA) 15 g agar-agar ad 1 l H2O	growth of L82, WCS417 and Bt
NYGA	5 g proteose peptone 3 g yeast extract 20 ml glycerol ad 1 l H2O, adjust pH to 7 18 g agar-agar	growth of *Pst*
Bacterial isolation solution	10 mM MgCl2 0.01% Silwet	Isolating bacteria from leaves post-harvest

Primers

Table 6: Primers used in this work

Primer name	Sequence (5'→3')	Description
Ubiquitin F	AGATCCAGGACAAGGAGGTATTC	*At* Ubiquitin
Ubiquitin R	CGCAGGACCAAGTGAAGAGTAG	*At* Ubiquitin
PDF1.2 F	CCAAGTGGGACATGGTCAG	*At* PDF1.2
PDF1.2 R	ACTTGTGTGCTGGGAAGACA	*At* PDF1.2
PR1 F	CTACGCAGAACAACTAAGAGGCAAC	*At* PR1
PR1 R	TTGGCACATCCGAGTCTCACTG	*At* PR1
VSP2 F	GTTAGGGACCGGAGCATCAA	*At* VSP2
VSP2 R	AACGGTCACTGAGTATGGGT	*At* VSP2
AZI1 F	ACAGAAAGCTTCCATCTGGTT	*At* AZI1
AZI1 R	ACAAATTAAGATTGATACATAAACT	*At* AZI1
EARLI1 F	AGTCCTAAGCACAAGCCTGT	*At* EARLI1
EARLI1 R	TCTGAGAGCATCGATAGGACA	*At* EARLI1
FMO1 F	CTTCTACTCTCCTCAGTGGCAAA	*At* FMO1
FMO1 R	CTAATGTCGTCCCATCTTCAAAC	*At* FMO1
UGT76B1 F	TGGAAGATCGGATTGCATT	*At* UGT76B1
UGT76B1 R	CCTTCATGGGCATAATCCTC	*At* UGT76B1
VSP1 F	TAGCCTTGTGAAGAAAGGGTACAAC	*At* VSP1
VSP1 R	AAGTAGAGTGGATTTGGGAGCTTAAA	*At* VSP1

Instruments

Table 7: Instruments used in this work

Device	Model	Manufacturer
Centrifuges	Heraeus Fresco 21	Thermo Fisher Scientific (Waltham, USA)
	Centrifuge 5415 D	Eppendorf (Hamburg, Germany)
Gel electrophoresis chamber	PerfectBlue Horizontal Minigelsystems	Peqlab/VWR (Radnor, USA)

Gel station	BIO-Print M1 gel documentation system	Vilber Lourmat (Eberhardzell, Germany)
Tissuelyser	Retsch Kugelmühle	Retsch, Haan, Germany
PCR cycler	Mastercycler nexus	Eppendorf (Hamburg, Germany)
Photometer	NanoDrop ND-1000	Nanodrop Technologies/Thermo Fisher Scientific (Waltham, USA)
qPCR cycler	Applied Biosystems 7500 Fast Real-Time PCR system (ABI 750 Fast)	Applied Biosystems, Freiburg, Germany
Microscope	Zeiss Axio Observer. Z1	Zeiss (Oberkochen, Germany)
Rotator	intelli-mixer rotator with vortexer	Neolab (Heidelberg, Germany)
Freeze Dryer	Alpha 2-4 LD Plus	Martin Christ Gefriertrocknungsanla-gen, Osterode, Germany

Software, R packages and web-tools

Table 8: Software and web-tools used in this work

Software	Version/source	Application
Microsoft office	Word, Excel, Powerpoint	Data analysis
LibreOffice	LibreOffice calc	Data analysis
7500 Fast System SDS Software	Version 1.3.1.21	qPCR control and raw data generation
Primer BLAST	https://www.ncbi.nlm.nih.gov/tools/primer-blast (Ye et al. 2012)	primer design for qPCR

Endnote	X8	reference management
R	v.3.6.3 (R Development Core Team, 2020)	Data analysis
Phyloseq (R)	1.3 (P. J. M. a. S. Holmes, 2013)	Microbial composition analysis
ggplot2 (R)	3.3.5 (H. Wickham, 2016)	graph design
vegan (R)	2.5.6 (Jari Oksanen, 2019)	alpha-diversity analysis
DESeq2 (R)	1.26.0 (Love, 2014)	identification of ASVs
gridExtra (R)	2.3 (Auguie, 2017)	graph design
dplyr (R)	1.0.5 (Hadley Wickham, 2020)	data manipulation
phangorn (R)	2.5.5 (Schliep, Potts, Morrison, & Grimm, 2017)	establishing phylogenetic distances
Biostrings (R)	2.54.0 (Pagès H, 2024)	data manipulation
ggthemes (R)	4.2.0 (Arnold, 2022)	graph design
RColourbrewer (R)	1.1.2 (Brewer, 2022)	graph design
tidyr (R)	1.1.2 (H. Wickham et al., 2019)	data manipulation
Cowplot (R)	1.1.0 (Wilke, 2020)	graph design
ggpubr (R)	0.4.0 (Kassambara, 2020a)	graph design
rstatix (R)	0.6.0 (Kassambara, 2020b)	statistical analysis
purr (R)	0.4.0 (Wickham H, 2022)	data manipulation
stringr (R)	1.4.0 (Hadley Wickham, 2019)	data manipulation
VennDiagram (R)	1.7.2 (H. Chen, 2022)	graph analysis
dada2 (R)	1.14.1 (Callahan BJ, 2016)	identification of ASVs

3. METHODS

Plant material and growth conditions.

Arabidopsis plants used for this study are all based on the Col-0 background. All plants were grown from synchronised seeds. Plants were grown on normal potting soil mixed with silica sand (grain size 0,6-1,2mm) at a ratio of 5:1. For IR experiments seeds were surface-sterilized with 75% ethanol twice for 4 minutes and grown on ½ Murashige and Skoog medium for 10 days (d) prior to treatment and transfer to soil. Plants were grown in a 10-hour (h) day light regimen and a light intensity of 100µmol m^{-2} s^{-1} photosynthetically active photon flux density at 22°C during light periods and 18°C during dark periods. Relative humidity was kept at >70%.

IR elicitors, pathogens and treatments

For elicitation of PGPR IR, two different bacterial strains were used: *Pseudomonas simiae* WCS417r (C. M. Pieterse, S. C. van Wees, E. Hoffland, J. A. van Pelt, & L. C. van Loon, 1996) and *Bacillus thuringiensis* (Heimpel & Angus, 1958). For root treatment, bacteria were grown on NB plates for 24 h and suspended in 10mM $MgCl_2$ to a final concentration of 2x 10^8 colony forming units (cfu) mL^{-1}, assuming that an OD_{600} =1 corresponds to 10^9 cfu mL^{-1}. To induce IR in Arabidopsis, the roots of 10-day-old seedlings were placed in wells of 96-well plates containing one of the bacterial suspensions or a sterile 10mM $MgCl_2$ control solution, each supplemented with 0.01% Tween-20 (v:v). After 1 h of incubation, the seedlings were placed in pots with soil and grown to an age of 34 d. On the 34th day after sowing, the leaves of the plants were either harvested for further analysis (ten plants) or inoculated with 10^5 cfu mL^{-1} of *Pseudomonas syringae* pathovar *tomato* (*Pst*) (also ten plants), which was maintained and used for analysis of infection severity as previously described (Wenig et al., 2019). To determine bacterial growth in the plants, *Pst* titres were determined 4 days post-inoculation (dpi). To this end, three leaf discs per sample were punched out of the infected leaves and were incubated in 10mM $MgCl_2$ + 0,01% Silwet (v:v) for 1 h at 600 revolutions per minute (rpm). This was done with three samples per condition and biological replicate. The resulting bacterial suspensions were serially diluted in steps of 10-fold. 20 µl per dilution were plated on NYGA agar plates with rifampicin at a concentration of 50mg/l and Kanamycin at a concentration of 50mg/l (Wenig et al.,

2019) and incubated for 2 d at room temperature. Bacterial titres were calculated based on the number of bacterial colonies formed.

To sample material for qPCR, the third and fourth leaf of control and WCS417/*Bt*-treated plants were infected with *Pst* and the leaves where either harvested before infection (T0) or two (T2h), four (T4h) or six (T6h) hours after infection. For qPCR primers for the genes *EARLI1, AZI1, FMO1, PR1, UDP-DEPENDENT GLYCOSYLTRANSFERASE 76B1 (UGT76B1), VSP1* where used (Table 6) (Berger, Mitchell-Olds, & Stotz, 2002; Griebel & Zeier, 2008; von Saint Paul et al., 2011).

To check how many bacteria adhere to the roots, additional plants were treated with WCS417 as described before and planted into potting soil. After 5 minutes, 1h and 1 d, the plants were removed from the soil, cut, and roots and leaves were placed separately into an 10mM $MgCl_2$ + 0,01% Silwet (v:v) solution for 1h at 600 rpm and serial dilutions were plated as described before. Two days later, bacterial titres were calculated based on the number of bacterial colonies formed. To monitor the movement of fluids along the seedling and reproduce the possible mechanism of bacteria reaching the phyllosphere, 10 d old seedlings were incubated in the wells of 96 well plates filled with 10mM $MgCl_2$ solution stained with aqueous iodine for 1 h. Fotos were taken either of the whole plantlets or of dissected plantlets cut either along the longitudinal axis or at a crosswise section.

In addition, to confirm the presence of WCS417 in the leaves of the plant, the growth of WCS417 on the leaves was monitored after the root-treatment. To this end, leaves were harvested 5 min, 1 h and 1 d after the treatment, leaf discs punched out and the bacterial titres were determined as described before, using rifampicin-containing NYGA agar plates.

Leaf inoculations were performed using 4-5-week-old plants. *Flavobacterium sp.* was obtained as strain Leaf82 from the *At*-LSPHERE synthetic community (Bai et al., 2015) and maintained on NB medium. Syringe infiltration was performed using 10^5 cfu mL^{-1} of bacteria in 10 mM $MgCl_2$. Spray inoculation was performed using 10^8 cfu mL^{-1} of bacteria in 10 mM $MgCl_2$ supplemented with 0.01% Tween-20 (v:v). *In planta* bacterial titres were determined as described above by counting plate-grown bacterial colonies derived from inoculated leaves. The colonies of WCS417 and Leaf82 were distinguished based on colour differences, as WCS417 forms opaque, white colonies while Leaf82 forms opaque orange colonies.

SAR was induced in 4-5-week-old plants as previously described (Wenig et al., 2019) except that WCS417 or *Bt* were used for the primary inoculation of the first two true leaves of the plants by syringe infiltration of 10^6 cfu mL^{-1} of bacteria in sterile 10 mM $MgCl_2$. 10^6 cfu mL^{-1} of *Pst* carrying the effector *AvrRpm1* was used as the positive control and 10 mM $MgCl_2$ as the negative control treatment (Wenig et al., 2019). Three d later, the establishment of SAR was tested by a secondary infection of the third and fourth true leaf of the plants with 10^5 cfu mL^{-1} of *Pst*. *Pst* titres were determined at 4 dpi as described above.

Bacterial confrontation assay

The bacterial confrontation assay was performed on NB-agar. A vertical line of one bacterium was streaked with a heat-sterilised loop directly onto the agar. The second bacterium was applied as a perpendicular line with a heat-sterilised infection loop on top of the other. The bacteria were grown at 25°C for two days.

RNA extraction, and RT-qPCR analysis

For RNA as well as DNA isolation each, one leaf per plant, either the 3rd or fourth true leaf of in total 10 plants per treatment were harvested, resulting in one pooled sample per treatment and replicate. That corresponds to 100-200ng of leaf material. RNA was isolated with RNA extraction buffer (Table 5). cDNA was generated with SuperscriptII reverse transcriptase. Quantitative PCR (qPCR) was performed using the Sensimix SYBR low-rox kit on a 7500 real-time PCR system (Applied Biosystems, Foster City, USA). Primers that were used for qPCR are listed in Table 6. Transcript accumulation of target genes was analysed using Relative Quantification with the 7500 Fast System Software 1.3.1.

DNA-Isolation, PCR and amplicon sequencing

For DNA isolation, the harvested plant material was freeze-dried for 24 h at -40°C and 0.12mbar. DNA isolation was performed utilizing the FastPrep Soil Kit according to manufacturer's instructions after an additional step of leaf grinding using a tissue lyser and glass beads (1mm diameter) at 25Hz for two minutes (Pfeilmeier et al., 2021). Following DNA extraction, the variable regions V5-V7 of the bacterial 16S rRNA gene were amplified by PCR using 10 ng of DNA per reaction and the primers 799F and 1193R from (Bulgarelli et al., 2012; Chelius & Triplett, 2001).

Three independent PCR reactions were performed per DNA sample using the following conditions: 98°C for 30 s, 98°C for 10 s, 58°C for 20 s, 72°C for 20 s, 72°C for 2 m. Steps 2-4 were repeated 25 times. The resulting PCR amplicons were subjected to gel electrophoresis to separate amplicons derived from bacteria and chloroplasts, since chloroplasts yield longer amplicons than bacterial DNA. The DNA amplicons derived from the bacterial 16S rRNA gene were extracted from the gels using the QIAquick Gel Extraction Kit. After determination of the DNA concentration of each amplicon, the 16S rRNA gene amplicons from 3 PCR-replicates per sample were pooled at equimolar amounts. The fragment sizes and concentrations of the pooled samples were determined on a Fragment analyzer 5200 using the DNF-473-Standard Sensitivity NGS Fragment Analysis Kit. The indexing PCR was performed under the following conditions: 98°C for 10 s, 55°C for 30 s and 72°C for 30 s and final extension at 72°C for 5 min. Each PCR reaction contained 1x NEBNext High Fidelity Mastermix, 10 ng of template DNA and index primer 1 (N7xx) and index primer 2 (N5xx) of Nextera XT Index Kit v2 Set according to the manufacturer`s instructions. All samples were purified using MagSi NGSprep Plus Beads. Samples were validated and quantified on a Fragment analyzer 5200 using the DNF-473-Standard Sensitivity NGS Fragment Analysis Kit, diluted and pooled to a final concentration of 4 nM for the sequencing run on an Illumina MiSeq using the MiSeq Reagent Kit v3 (600-cycle). Demultiplexing was done using the MiSeq Reporter Software v 2.6.

Statistical analysis

All statistical analyses were done using R version 3.6.3. (R Development Core Team, 2020). The analysis was performed separately for WCS417 as well as *Bt* treated plants, since the results were published separately. For the analysis of bacterial titres, a Shapiro Wilk test for normal distribution showed that the cfu counts resulting from the infection assays did not follow normal distribution ($\alpha=0.05$) (SHAPIRO & WILK, 1965). Therefore, a Kruskal-Wallis test was used to test for significance at $\alpha=0.05$. For qPCR analysis, the same steps were taken during analysis (Kruskal & Wallis, 1952). For the analysis of the primed states of the genes *AZI1, EARLI1, FMO1, PR1, UGT76* and *VSP1,* the highest value of the time point T2h-T6h (normalised to the respective control treatment) per experiment and treatment was taken and these values were merged and then statistically compared to the merged corresponding T0-values as well as the control-sample value. Since a normal distribution was not given (Grubbs, 1969),

significant differences between the relative quantification (RQ) according to treatment were tested with a Kruskal-Wallis test.

Amplicon data analysis

Pre-processing of the amplicon data was performed using the package “dada2”, including trimming, removal of low-quality reads, merging of reads, chimera removal and taxonomic assignment based on the Silva Seeds v.138 database (Callahan BJ, 2016; Yilmaz et al., 2013). The reads were truncated at the first occurrence of a quality score ≤2. Filtering criteria were a length of at least 270 bp in forward reads and 150 bp in reverse reads, and absence of ambiguous bases in the remaining reads. For samples treated with WCS417 and control-treated samples, in total, 718,990 reads were processed in 14 samples and after preprocessing 508,154 reads remained, which were assigned to taxa based on Amplicon Sequence Variants (ASVs). For samples treated with *Bt* and control-treated samples 920,677 reads were processed in 14 samples and after preprocessing, 615,614 reads remained, which were assigned to 798 taxa. Phylogenetic trees were fitted based on DECIPHER (Wright, 2016). To control for uniformity of DNA isolation and PCR bias as well as contamination, a commercially available Microbial Community Standard by ZymoBIOMICs was prepared as an additional sample and handled in the same fashion as the other samples after the freeze-drying step.

Prior to analysis of the data, the *Pst* titre reductions triggered by each treatment were controlled as compared to the appropriate controls. This was done to check whether PGPR IR was elicited and to exclude data from samples derived from experiments, in which PGPR IR was not significant. Data from the remaining 6-7 replicates per treatment were analysed using the R packages Vegan, Phyloseq, DESeq2, and Phangorn (P. J. M. a. S. Holmes, 2013; Jari Oksanen, 2019; Love, 2014; Schliep et al., 2017). Alpha diversity was calculated using the Shannon’s- as well the Simpson’s index (SIMPSON, 1949; Spellerberg & Fedor, 2003). Statistically significant differences of alpha-diversity were calculated utilizing a pairwise t-test, since a previous Shapiro-Wilk test did not show any indication for a deviation of normality. Regarding the WCS417 data set, analysis of the obtained data indicated one outlier sample per treatment. This was confirmed by a Grubbs’ test (Grubbs, 1969), which was significant for the number of observed ASVs for the respective samples of the treatments, near significant (WCS417) or significant (control) regarding the Shannon’s, and significant for the sample from the control-treatment regarding the Simpson’s

Index. This concerns the samples control treatment, replicate 2 and WCS417 treatment, replicate 6. Those were removed from the dataset preceding further analysis (p-values of Grubb's test, see Table 9). The same test regime for outliers was applied to the *Bt* data set and two samples were removed with the same reasoning (control treatment, replicate 2 and *Bt* treatment, replicate 5).

To address β diversity, the R package "DESeq2" was used: the data were transformed using the built-in function in DESeq2 by calling "variancestabilizingTransformation" (McMurdie & Holmes, 2014) and subsequently, a PCA was fitted using "plotPCA". Based on the resulting distance matrix, a MANOVA was performed to test for significant differences in the overall microbial community dependent on the treatment (Love et al., 2014; Pfeilmeier et al., 2021).

Differentially abundant ASVs were also determined using DESeq2 (Love et al., 2014; Pfeilmeier et al., 2021). The analysis was limited to ASVs present in at least three replicates; ASVs were considered as differentially abundant with an FDR-corrected p-value < 0.05.

Table 9: p-values of Grubb's test for outlier

Treatment	Index tested	*p*-value
Control	Observed ASVs	0.004088
WCS417	Observed ASVs	0.01975
Control	Shannon's	0.0015
WCS417	Shannon's	0.05038
Control	Simpson's	<0.0001
WCS417	Simpson's	0.2673

4. RESULTS

4.1 IR INDUCED BY WCS417

4.1.1 Pseudomonas simiae WCS417r propagates in the phyllosphere of Arabidopsis thaliana

P. simiae WCS417r, referred to below as WCS417, triggers systemic IR in *Arabidopsis,* reducing the propagation of pathogenic *P. syringae* pathovar *tomato* (*Pst*) in the leaves of the treated plants (C M Pieterse, S C van Wees, E Hoffland, J A van Pelt, & L C van Loon, 1996). To trigger systemic IR, WCS417 is applied to the soil surrounding *Arabidopsis* roots. Here, I investigated if WCS417 also induces resistance when applied to plants by alternative methods. To this end, 10-day-old, sterile-grown seedlings were treated by dipping their roots in a WCS417 suspension. Subsequently, plants were transferred to soil. Since viable WCS417 bacteria were detected in the phyllosphere of the treated plants, a possible propagation of WCS417 in *Arabidopsis* roots and leaves was investigated. To this end, *Arabidopsis* plants were treated with WCS417 via root-dip inoculation and transferred to soil one hour later. After 5 minutes, 1h and 1d, the plants were removed from the soil and the WCS417 titres assessed in root and leaf tissues in a plate-based assay, using rifampicin to select for WCS417 (Pieterse *et al.*, 1996). WCS417 titres were lower in the leaves than in the roots but were evident from the first sampling timepoint on (Figure 7A). The roots were colonized in high numbers (> $1x10^3$ cfu per sample) from the first timepoint on with the highest values detected 1h after transfer of the treated plants to soil. Similarly, WCS417 titres reached a maximum in the leaves at 1h after transfer to soil and were reduced to $1x10^4$ cfu per sample 1d later (Figure 7 A). While uptake of *Pseudomonas* spp. through the xylem cannot be excluded (Kong et al., 2020; Misas-Villamil, Kolodziejek, & van der Hoorn, 2011; Paauw et al., 2023), it is equally possible that bacteria spread from the roots to the leaves via capillary water movement on the surface of the hypocotyl. When

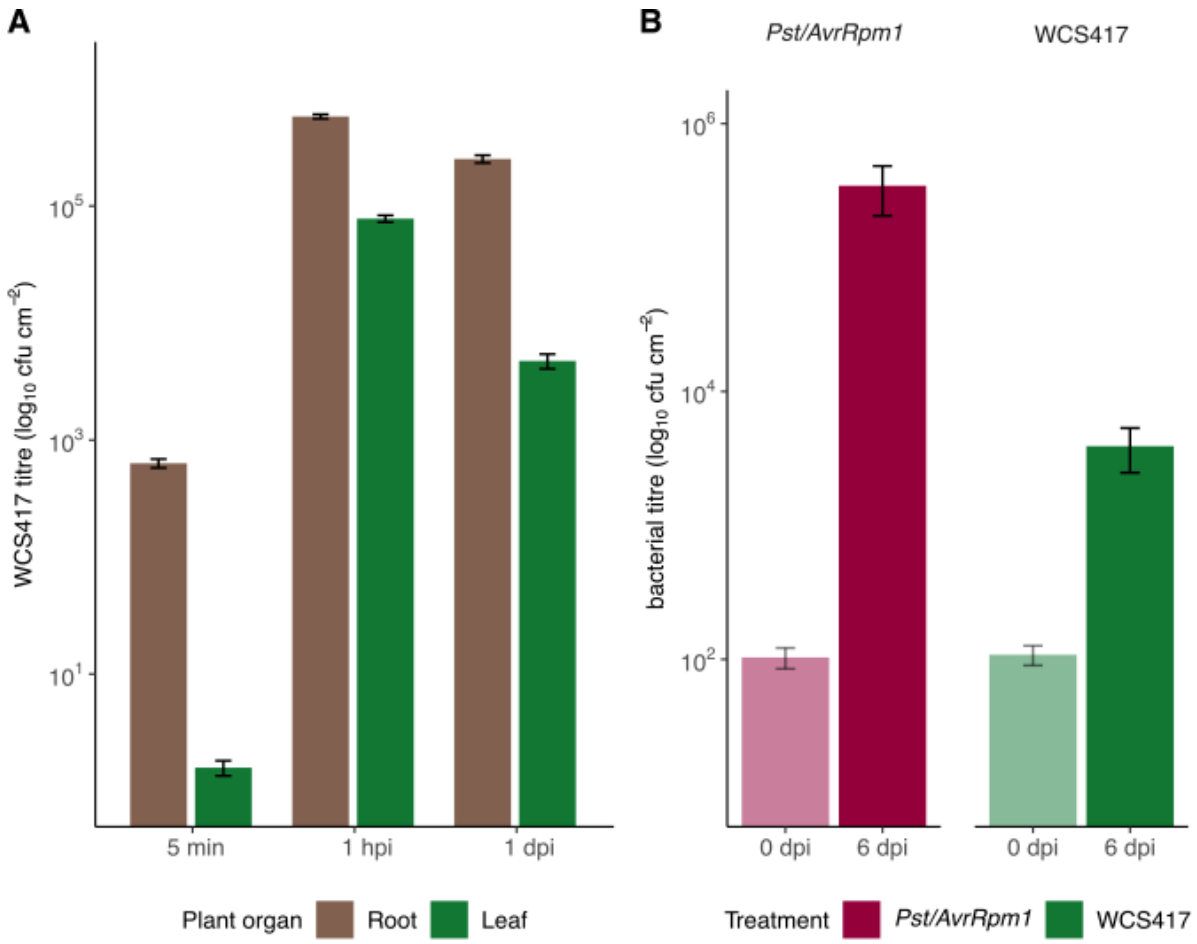


Figure 7: Proliferation and mobility of P. simiae WCS417r (WCS417) on Arabidopsis thaliana plant organs.

(A) Adherence and proliferation of WCS417 in/on Arabidopsis roots and leaves 5 minutes, 1 hour (h), and 1 day (d) post-inoculation (pi) of plant roots with WCS417 by root-dip treatment. Brown bars indicate bacterial titres in/on the roots, green bars indicate bacterial titres in/on the leaves. The height of the bars represents the mean ± SE of two biologically independent experiments, including three replicates each. (B) Growth of bacteria in A. thaliana leaves. Leaves of 4-5-week-old A. thaliana plants were syringe-infiltrated with Pseudomonas syringae pathovar tomato (Pst) containing the effector AvrRpm1 (positive control, red bars) or WCS417 (green bars) as indicated above the panel. The resulting in planta titres of these bacteria were monitored 2 h after inoculation (0 dpi) and six days later (6 dpi). Bars represent the mean of two biologically independent experiments, including three replicates each ± SE.

treated by root-dip with iodine-stained water, *Arabidopsis* seedlings take up most of the dye via capillary water movement on the surface of the hypocotyl (Figure 8). Next, the question, whether WCS417 propagates in the phyllosphere of *Arabidopsis* was addressed. To this end, leaves were inoculated with 10^5 cfu/mL of WCS417 by syringe-infiltration and the resulting bacterial titres were determined 2 h (0 dpi) and 6 d later. As a positive control *Pst* carrying the effector *AvrRpm1* was included. Although the avirulent, pathogenic control bacteria *Pst/AvrRpm1* grew to higher titres, a significant increase in WCS417 titres at 6 dpi as compared to 0 dpi was detected, indicating active

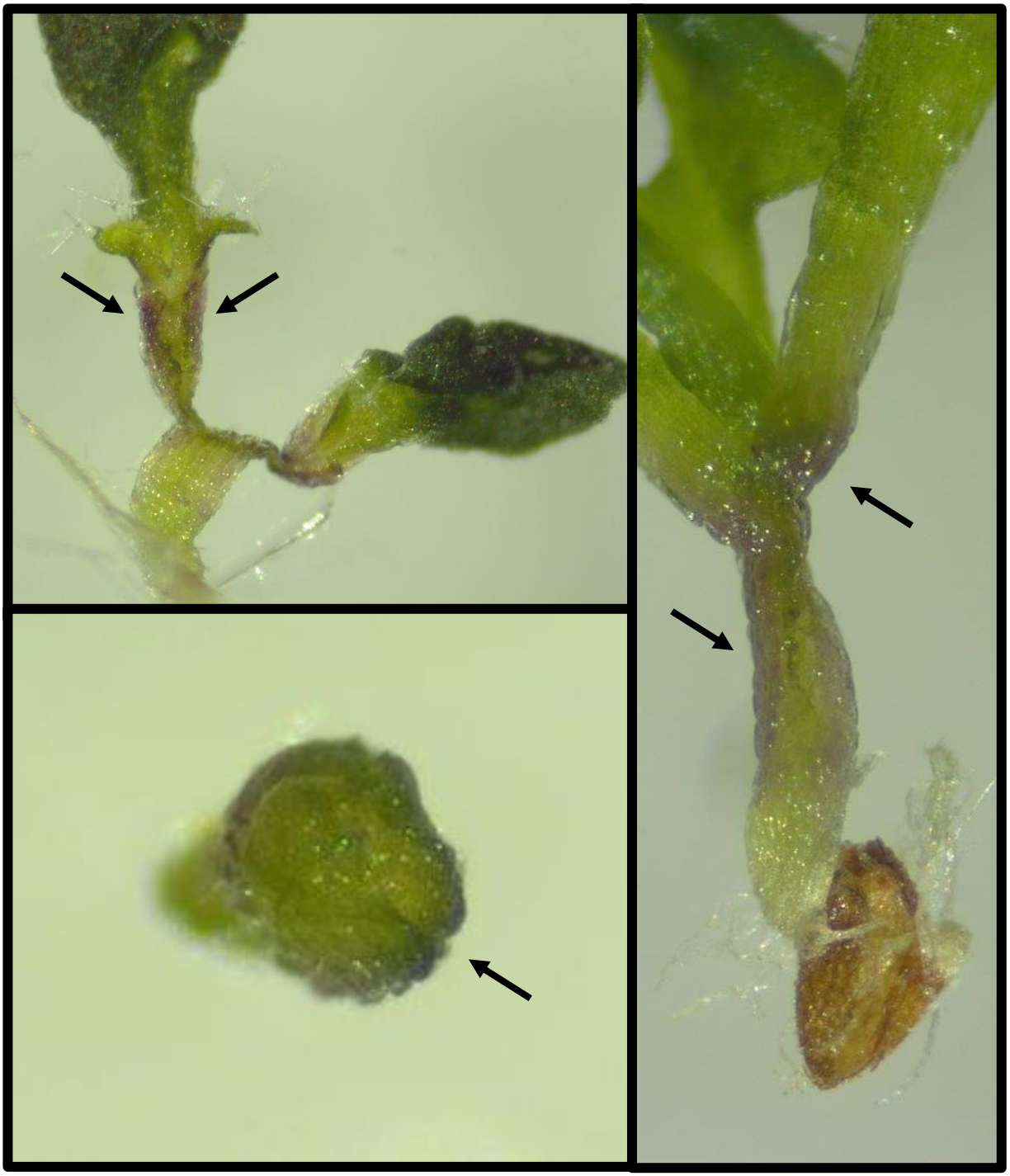


Figure 8: Water uptake upon root-dip inoculation of seedlings.

10-day old, sterile-grown Arabidopsis seedlings were treated by root-dip inoculation with aqueous iodine in water for 1h. Brown-blue staining corresponds to starch, which displays a blue colour when it comes in contact with iodine. Arrowheads indicate positions where staining is observed. (A) Seed, hypocotyl, and proximal end of cotyledons. (B) Longitudinal section of a stained Arabidopsis seedling. (C) Hypocotyl cross section.

proliferation of WCS417 in *Arabidopsis* leaves (Figure 7). Thus, root-dip inoculation of roots of *Arabidopsis* seedlings resulted in uptake of bacteria via capillary movement of

the inoculum on the surface of the hypocotyl and subsequent proliferation of WCS417 in the phyllosphere.

4.1.2 WCS417 elicits local induced resistance in the Arabidopsis phyllosphere

In the following experiment, I studied whether root-dip inoculation of *Arabidopsis* with WCS417 enhanced the resistance of the leaves to pathogenic *Pst.* As described above, the roots of 10-day-old, sterile-grown seedlings were treated with WCS417 or with sterile 10mM $MgCl_2$ as a negative control and transferred to soil. 24 d later, leaves of the resulting plants were inoculated with *Pst*, *in planta* titres of which were determined at 4 dpi. Root-dip inoculation with WCS417 reduced the growth of the *Pst* inoculum in the leaves as compared to that in control plants (Figure 9 A). Because WCS417 did not appear to directly inhibit *Pst* growth in a plate-based interaction assay (Figure 10) the data suggest that treatment of *Arabidopsis* roots and associated propagation of WCS417 in the *Arabidopsis* phyllosphere triggers IR against *Pst.*

Next, I sought to confirm that WCS417-triggered IR was mediated by the plant immune system. In contrast to SAR, which is classically associated with SA signaling, WCS417-triggered systemic IR has previously been associated with JA signaling as well as an SA-independent function of NPR1 (C M Pieterse et al., 1996; C. M. J. Pieterse et al., 2021; C. M. J. Pieterse et al., 1998; Pozo et al., 2008; Spoel et al., 2003). *VEGETATIVE STORAGE PROTEIN 1* (*VSP1*) is a marker gene of the JA signaling pathway (Creelman & Mullet, 1997; Guerineau et al., 2003). Here, it was tested whether local IR induction leads to changes in JA signaling by conducting RT-qPCR analysis of *VSP1* transcript accumulation. Additionally, a possible influence of IR on SA signaling was tested targeting the SA marker gene *PATHOGENESIS RELATED 1* (*PR1*) (van Loon, Rep, & Pieterse, 2006) and on the SAR-associated genes *AZI1* and *EARLI1* (Cecchini et al., 2015; Jung et al., 2009; K. Yu et al., 2013) as well as *FMO1* and *UGT76B1*.

For the analysis of gene expression changes which were induced during IR, leaves of WCS417- and control-treated plants were sampled before the challenge infection; these samples were designated as T_0. At this time point, the transcript levels of all tested genes were comparable in WCS417- and control-treated plants (Figure 9). Often, full defence responses are not directly/constitutively activated after induction of IR. Rather, priming of defence responses leads to a stronger and faster response after

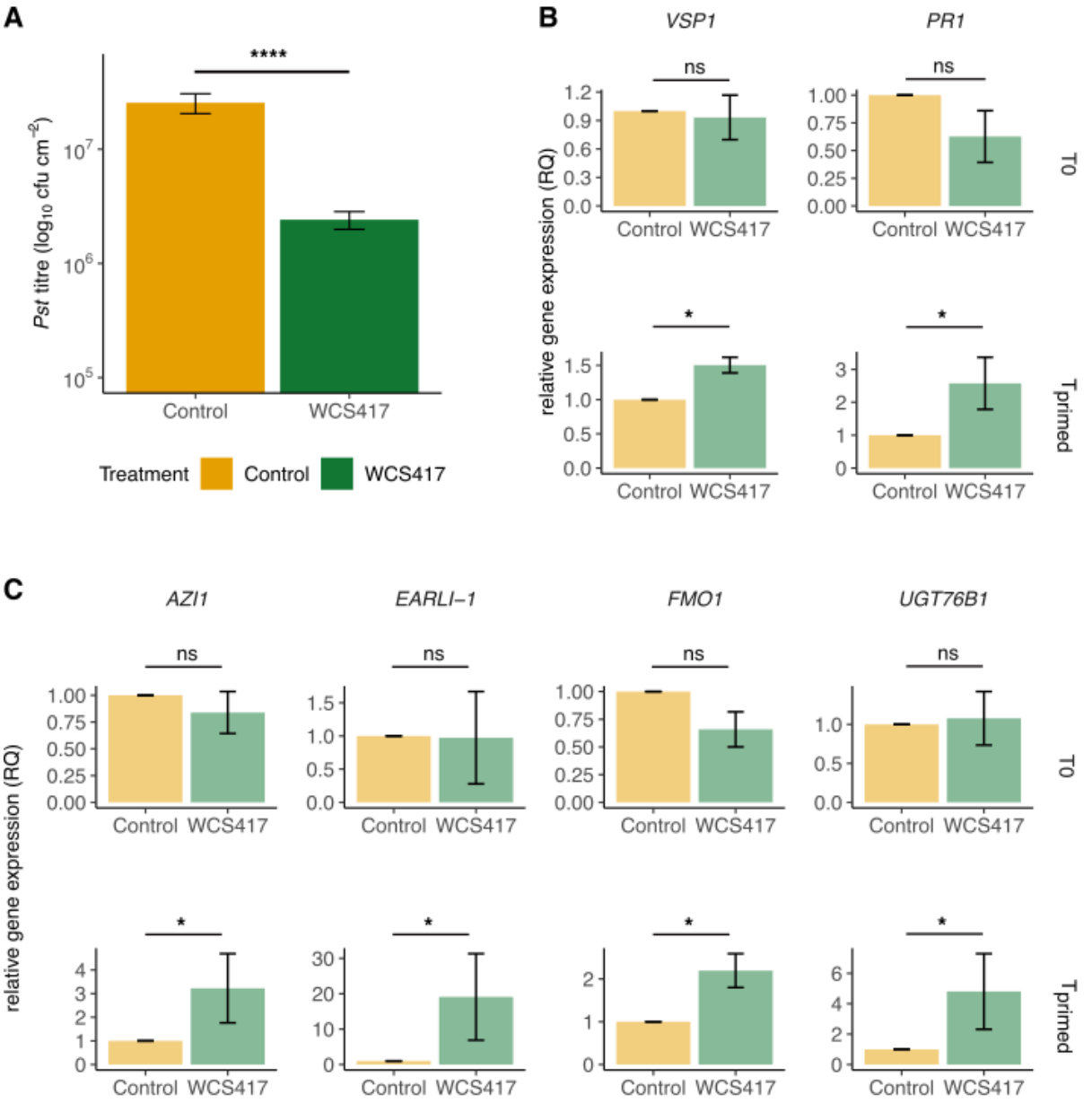


Figure 9: *WCS417 triggers local induced resistance (IR) in Arabidopsis with priming of the JA, SA, and SAR marker genes VSP1, PR1, AZI1, EARLI-1, FMO1, and UGT76B1.*

*The roots of 10-day-old, sterile-grown A. thaliana seedlings were inoculated with WCS417 (green bars) or a corresponding control solution (yellow bars). Following 3.5 weeks on soil, the leaves of the treated plants were infiltrated with Pst. (A) In planta Pst titres at 4 dpi. Bars represent the mean of three biologically independent experiments, including three replicates each ± SE. Asterisks indicate significant differences between the treatments indicated by the corresponding lines (Kruskal-Wallis test, ****, p <0.0001; ns, not significantly different). (B/C) Transcript accumulation of VSP1 and PR1 (B) and of AZI1, EARLI-1, FMO1, and UGT76B1 (C). Transcript accumulation was evaluated by RT-qPCR in leaves of plants treated as in (A) and sampled before (T0) or after infection (Tprimed). Tprimed indicates a merged analysis of maximum RQ-values per biologically independent experiment at 2, 4, and 6 hpi (Supplementary Figure S4). Transcript accumulation was normalized to that of UBIQUITIN. Bars represent mean values of three biologically independent experiments ± SE. Statistically significant differences were evaluated using a Kruskal-Wallis test, *, p <0.05.*

a pathogenic challenge as compared to unprimed plants, which also culminates in enhanced resistance (Uwe Conrath et al., 2015; Martinez-Medina et al., 2016; Mauch-

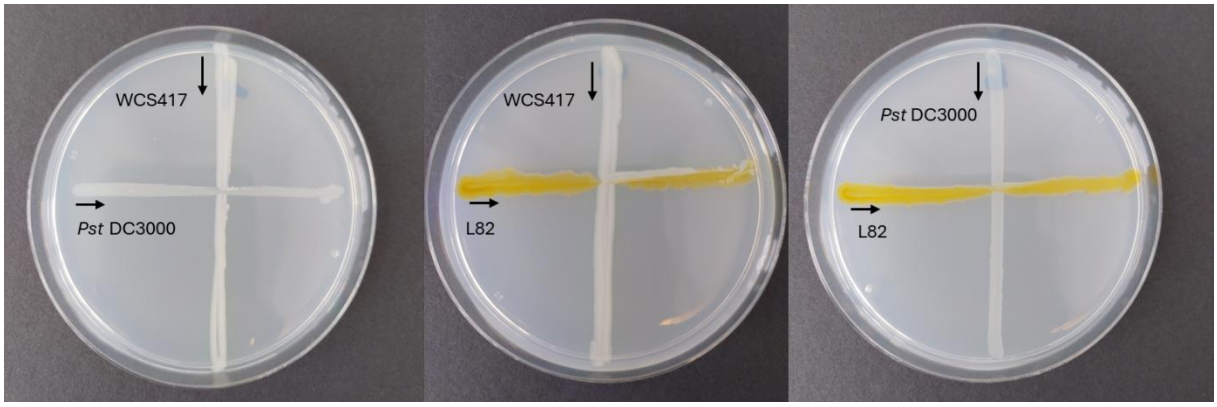


Figure 10: Microbial confrontation assay.

Bacterial strains were streaked out crosswise on NB-plates and grown 2 d at 25°C. Names besides the arrows indicate bacterial strains streaked out. Vertical bacterial strains were applied first, the perpendicular strains second.

Mani, Baccelli, Luna, & Flors, 2017). Because WCS417-triggered systemic IR is executed as a form of priming (C. M. Pieterse et al., 2014; Verhagen et al., 2004), I assessed primed gene expression changes during IR at 2, 4, and 6 h post-inoculation (hpi) of the treated plants with *Pst.* Priming was detected in multiple biologically independent experiments but did not always peak at the same point in time after inoculation (Supplementary Figure 1). For this reason, I analysed the priming peaks per experiment in a merged analysis of T_{primed}. In this analysis, WCS417-treated plants displayed a significantly higher transcript level than control-treated plants of all tested genes (Figure 9), confirming a priming effect of IR on the transcript accumulation of *VSP1, PR1, AZI1, EARLI1*, *FMO1*, and *UGT76B1*. Thus, the data suggest that WCS417-triggered IR is associated with priming of JA, SA, and SAR-associated gene expression changes.

4.1.3 WCS417-triggered local IR depends on SA- and SAR-associated components of the plant immune system

WCS417-triggered systemic IR has been shown to depend on functional JA defences, but not on the accumulation of SA (C M Pieterse et al., 1996; C. M. J. Pieterse et al., 1998; Pozo et al., 2008). Here, I investigated WCS417-triggered IR in *Arabidopsis* mutants with compromised MYC2-dependent JA defences *(jin1/myc2*) and also in mutants with compromised SA accumulation (*SALICYLIC ACID INDUCTION*

DEFICIENT (sid2-1)) and signaling (*npr1-1*) (Berger, Bell, & Mullet, 1996b; Cao et al., 1997; Pozo et al., 2008; Mary C Wildermuth et al., 2001). IR was induced as described above, and the leaves of the plants were inoculated with *Pst.* Col-0 wild type supported less *Pst* growth in the leaves of plants pre-treated with WCS417 as compared to the controls, confirming that IR was induced (Figure 11A/B). As reported before (Nickstadt, 2004), the *jin1* (*myc2*) mutant supported less *Pst* growth than Col-0 wild type plants. The absolute titres of *Pst* in control-treated *jin1*-plants were similar to those of wildtype plants with functional WCS417-triggered IR (Figure 11 A). Similar to previous reports of WCS417 IR (Pozo et al., 2008), WCS417-triggered IR did not further lower bacterial titres in *jin1* mutant plants (Figure 11A). In contrast to IR without WCS417 accumulation in the leaves, however, WCS417-triggered IR in this instance was ineffective and even appeared to enhance *Pst* growth slightly and significantly in *sid2-1* mutant plants. WCS417-triggered IR was further dependent on functional NPR1 (Figure 11 A).

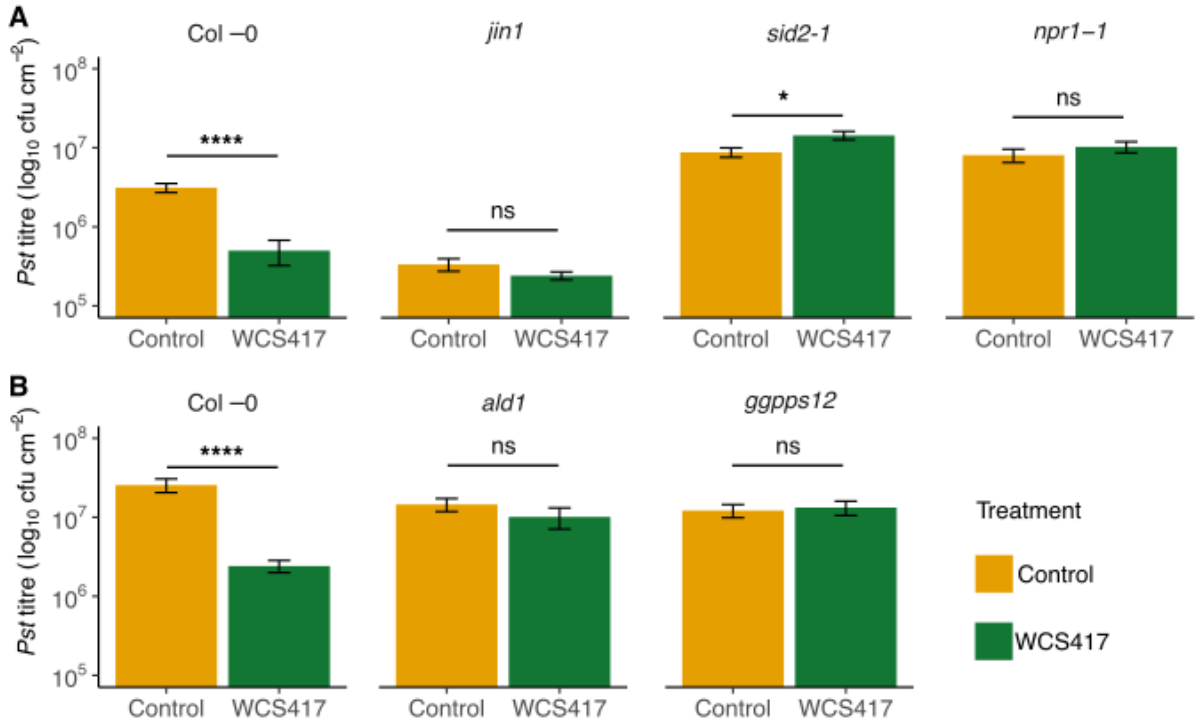


Figure 11: Characterization of the molecular requirements of WCS417-triggered local IR.

*The roots of 10-day-old seedlings of the genotypes indicated above the panels were inoculated with WCS417 (green bars) or a corresponding control solution (yellow bars). Following 3.5 weeks on soil, the leaves of the plants were inoculated with Pst. The resulting in planta Pst titres at 4 dpi are shown. Bars represent the mean of three biologically independent experiments with three replicates each ± SE. Asterisks indicate significant differences between the treatments indicated by the corresponding lines (Kruskal-Wallis test *, p <0.05, **, p <0.01, ***, p <0.001, ****, p <0.0001; ns, not significantly different).*

Together, the data suggest that WCS417-triggered IR after root-dip treatment with WCS417 accumulation in the leaves depended on MYC2 as well as on functional pathogen-induced SA accumulation and signaling.

Recent evidence further suggests roles of SAR-associated signaling intermediates in systemic IR (Cecchini et al., 2015; Shine et al., 2019). Here, the involvement of Pip-dependent pathways in IR was assessed by using *ald1* mutant plants with defects in Pip biosynthesis (Navarova et al., 2012). Additionally the involvement of SAR-associated volatile monoterpenes was tested by monitoring IR in the respective loss-of-function mutant *ggpps12* (Riedlmeier et al., 2017; Wenig et al., 2019). In comparison to the respective control treatments, WCS417 did not reduce growth of the *Pst* challenge inoculum in *ald1* and *ggpps12* plants, indicating that Pip and monoterpenes are essential in the realisation of immunity during WCS417-triggered IR (***Figure 11***B). Taken together, the data suggest that WCS417-triggered IR is dependent on SA, Pip, and monoterpenes, and might be triggered via a mechanism that is at least partially overlapping with SAR.

4.1.4 WCS417-triggered local IR changes the microbial composition of the phyllosphere

Defects in plant immunity have been shown to switch the role of certain bacteria from beneficial to pathogenic (Pfeilmeier et al., 2021). Chen et al. (2020) further illustrated a strong connection between plant immunity, the leaf microbiome, and plant health (T. Chen et al., 2020). Also, the PGPR *Bacillus velezensis* has been shown to enhance immunity in *Nicotiana tabacum* leaves by changing the phyllosphere microbiome (He Liu et al., 2022). These findings emphasise the importance of the plant immune status for the leaf microbiome and *vice versa*, and raise the question whether induced resistance influences the leaf microbiome.

To address this question, amplicon sequencing of the bacterial 16S rRNA gene in leaf samples from WCS417- and control-treated plants was performed. Bacterial communities of WCS417-treated plants on average contained 165 different ASVs per sample in comparison to 361 different ASVs per sample in control-treated plants (Figure 12 and Figure 13).

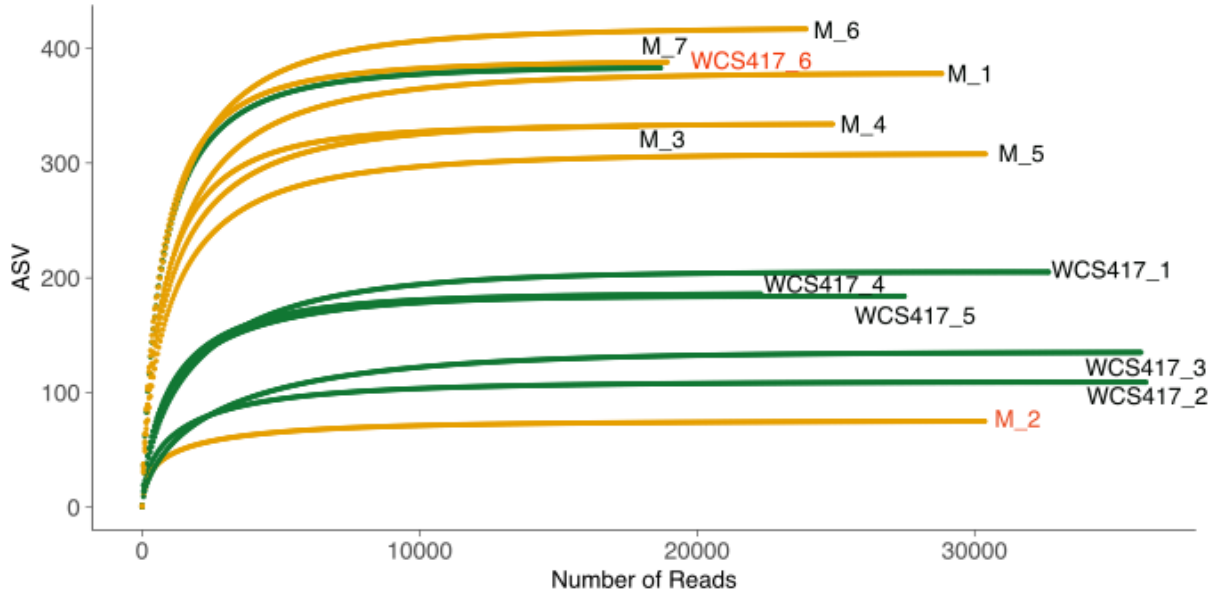
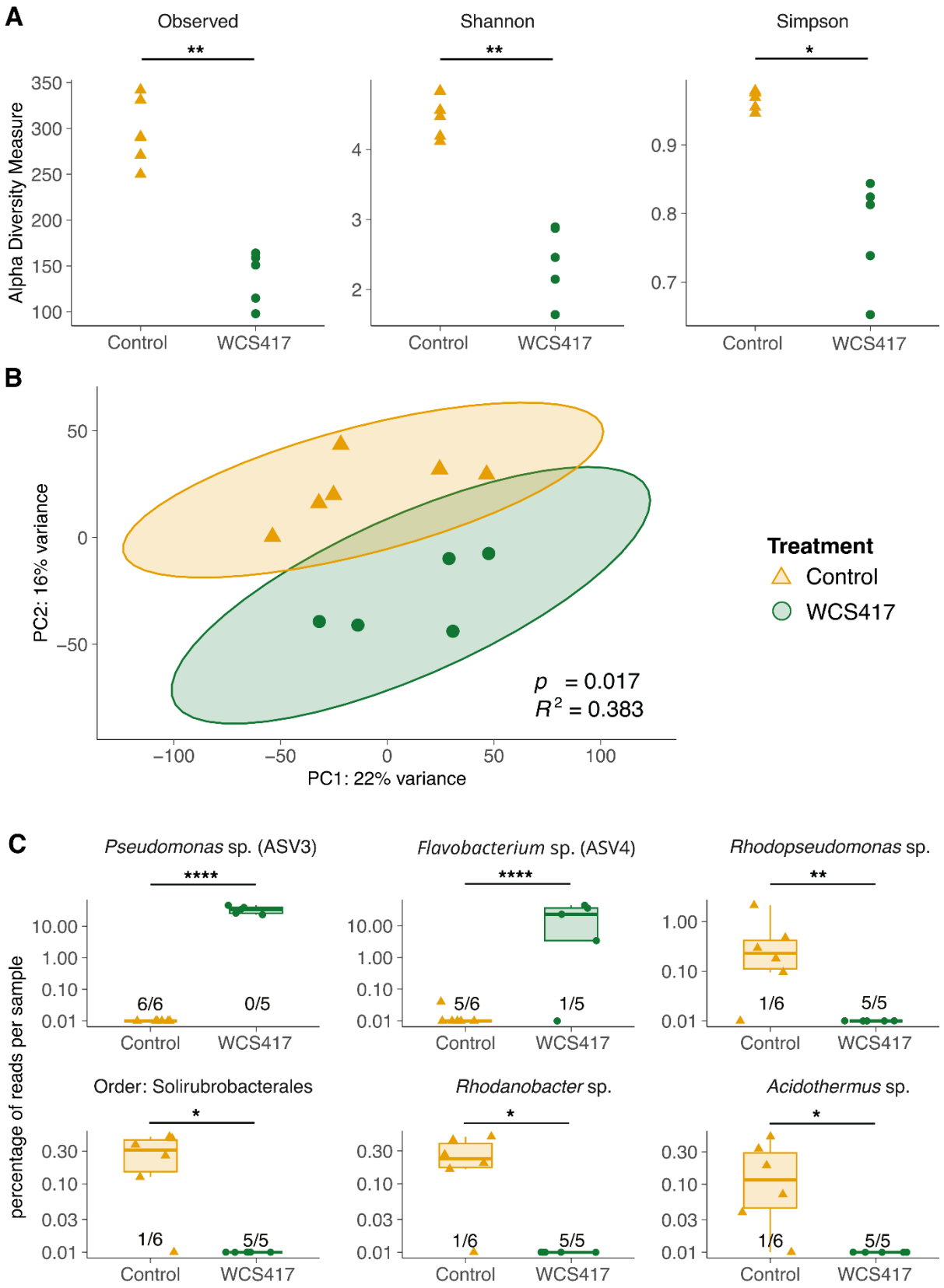


Figure 12: Rarefaction curves of 16S rRNA amplicon sequences in the phyllosphere of either WCS417- (green) or control-treated (yellow; M) plants.

The x-Axis represents the absolute number of sequenced reads; the y-axis represents the number of identified amplicon sequence variants (ASVs). Sample numbers are included next to the curves in the pattern "Treatment_SampleNumber", with M for Mock= control treatment. Identifiers in red represent statistically significant outliers (Grubb's test, see Supplementary Table S2 for details); data from these samples were excluded from further analysis.

Figure 13: (next page) Differences in the microbiome of the phyllosphere following WCS417 IR treatment in comparison to control-treated plants.

*Leaves of plants grown for 3.5 weeks on soil after root-dip inoculation with either 10 mM $MgCl_2$ (control treatment, yellow triangles) or WCS417 (green dots) were harvested and amplicon sequencing of the 16S rRNA gene was performed. (A) Principal Component Analysis of the overall microbial composition, PC1 and PC2 represent the respective principal components with the corresponding explained variance in percent. The p-value was calculated using a Fig11 cont.: MANOVA based on the Euclidian distance matrix of the PCA and was corrected for multiple testing using the Benjamini-Hochberg procedure. The effect size describes the percentage of variance explained by treatment. (B) α-diversity indices of phyllosphere microbiome following WCS417- or control-treatment: Number of observed ASVs (left) Shannon's Index (middle) and Simpson's Index (right). The y-axis represents the respective index value, and dots indicate the values of individual samples. Samples from WCS417-treated plants have significantly lower ASV-numbers as well as α-diversity indices than control-treated plants (pairwise t-test, *, p <0.05, **, p < 0.01). (C) Relative abundance of distinct bacterial species in the A. thaliana phyllosphere. Boxplots indicate average number of sequenced reads corresponding to the species indicated above the panels from five (WCS417) to six (control) samples in percentage of reads per sample ± min and max values. Numbers at the bottom of the boxplots indicate number of samples with zero read counts per species / total number of samples. Significance was calculated using a built-in Wald-test of the DESeq2-package with FDR correction following the Benjamini-Hochberg procedure *, p < 0.05, **, p < 0.01, ****, p < 0.0001*


A
Observed
Shannon
Simpson
**
**
*
Alpha Diversity Measure
350
300
250
200
150
100
4
3
2
0.9
0.8
0.7
Control
WCS417
B
PC2: 16% variance
50
0
−50
−100
−50
0
50
100
PC1: 22% variance
p = 0.017
R2 = 0.383
Treatment
Control
WCS417
C
Pseudomonas sp. (ASV3)
Flavobacterium sp. (ASV4)
Rhodopseudomonas sp.
****
****
**
percentage of reads per sample
10.00
1.00
0.10
0.01
6/6
0/5
5/6
1/5
1/6
5/5
Order: Solirubrobacterales
Rhodanobacter sp.
Acidothermus sp.
*
*
*
0.30
0.10
0.03
0.01
1/6
5/5
Control
WCS417

For this reason, I analysed ASV richness and evenness utilizing the Shannon's Index (Spellerberg & Fedor, 2003) and species richness as well as dominance of single ASVs using the Simpson's Index (Simpson, 1949).

The apparent lower species richness in WCS417-treated plants was confirmed by the Shannon's Index as well as the Simpson's index, which were both significantly lower in WCS417-treated than in control-treated plants (Figure 13A). Next, I assessed the similarity or divergence of the microbial composition of the different samples with regard to the abundance of the different ASVs using a principal component analysis (PCA). The PCA showed that the microbiome of plants treated with WCS417 clustered distinctly from that of control-treated plants (Figure 13B). Subsequently, I performed a MANOVA based on the distance matrix of the PCA to test for significant differences between the microbial composition following the different treatments. The phyllosphere microbiome of plants treated with WCS417 was significantly different from the phyllosphere microbiome of control plants. The treatment describes 38% of the differences between the treatments (R^2 = 0.383).

After this first explorative analysis of the data, I checked for occurrence of WCS417 on the leaves of the plants. Therefore, I examined the absolute numbers of ASV3, whose 16S rRNA gene sequence corresponded to that of WCS417. In WCS417-treated plants, the reads of ASV3 on the leaves made up ~25% of the reads per sample (Figure 13C). This confirms the findings described above that root-dip inoculation of *Arabidopsis* results in uptake and propagation of WCS417 in the plants' phyllosphere. ASV3 was not detected in the microbiome of control-treated plants, excluding cross-contamination between treatments during the local IR treatment.

13 different ASVs were present in all samples, of those, 12 stem from the phylum of Proteobacteria and one from the phylum of Actinobacteria. Concerning significant differences in the abundance of ASVs, WCS417-treated plants displayed differential abundance of 6 ASVs in comparison to control-treated plants (Table 10). Most of the differentially accumulating ASVs were less abundant in local IR-treated compared to control-treated plants. Also, most of the significantly different ASVs were detected at relatively low read count numbers of < 1% of all reads. Those ASVs comprise bacteria from the genera Rhodopseudomonas, Rhodanobacter, and Acidothermus as well as one bacterium from the Order Solirubrobacterales (Figure 13C). In contrast, one ASV besides the putative WCS417 (ASV3) was considerably enriched in the local IR-treated

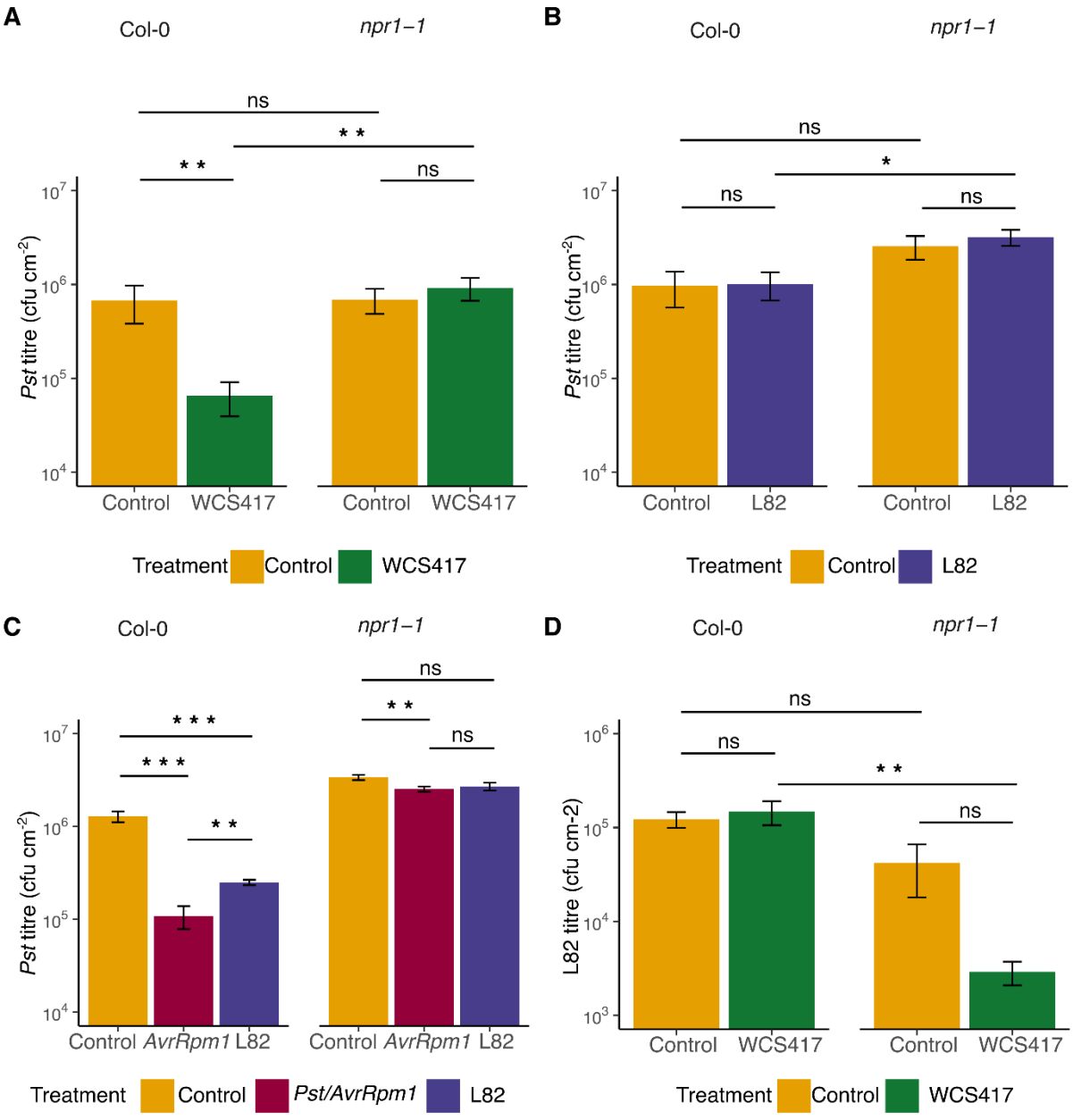


Figure 14: Local and systemic plant-microbe-microbe interactions.

*Leaves of 4-5 week old Col-0 wild type and npr1-1 mutant Arabidopsis plants (genotypes indicated above the panels) were infiltrated with WCS417 (green bars in A/D), At-L-Sphere Flavobacterium sp. Leaf82 (L82; purple bars in B/C), or a corresponding negative control solution (yellow bars in A-C) or with Pst/AvrRpm1 as a positive control (red bars in C). Two days later, the same leaves were infiltrated with Pst (A/B) or Leaf82 (D) or two systemic leaves were infiltrated with Pst (C), titres of which were determined at 4 dpi. Bars represent average in planta Pst (A/B/C) and Leaf82 (D) titres from 6 to 9 samples derived from two (D) to three biologically independent experiments (A/B/C) ± SE. Asterisks indicate significant differences between the treatments indicated by the corresponding lines (A/B/D: Kruskal-Wallis test, C: paired samples Wilcoxon test, *, p <0.05, **, p <0.01, ***, p <0.001; ns, not significantly different).*

plants. In four out of five samples from WCS417-treated plants, an ASV linked to Flavobacterium sp. was detected at an average of 28% of all reads per sample ranging from 3.5% to 39% (Figure 13C). By comparison, the same ASV was detected with 1 read in 1 control sample, and thus remained negligible on control-treated plants (Figure 13C). Thus, treatment of Arabidopsis with WCS417 was associated with a significant enrichment of the phyllosphere microbiome with *Flavobacterium* sp..

Table 10: Amplicon sequence variants (ASVs) with a significantly different relative abundance in the phyllosphere microbiome of WCS417-treated plants as compared to control-treated plants.

ASV	Genus	Padj.	log_2FoldChange	sum of all reads	Number of samples ASV is present in
ASV3	*Pseudomonas*	<0.0001	17.11	51708	5
ASV4	*Flavobacterium*	<0.0001	14.16	37538	5
ASV93	*Rhodopseudomonas*	0.0070	-8.37	770	5
ASV120	Order: Solirubrobacterales, Family: 67-14	0.0177	-7.48	411	5
ASV132	*Rhodanobacter*	0.0205	-7.20	355	5
ASV189	*Acidothermus*	0.0454	-6.91	277	5

4.1.5 Flavobacterium sp. Leaf82 induces Systemic Acquired Resistance (SAR) in Arabidopsis

Since WCS417 proliferated in *Arabidopsis* leaves, I tested if this proliferation was causative for IR. To this end, leaves of 4-5-week-old *Arabidopsis* plants were infiltrated with WCS417 or with 10 mM $MgCl_2$ as the negative control. Two days later, a challenge inoculation of the same leaves with *Pst* was performed. As expected, WCS417 treatment of the leaves caused a reduction of *Pst* proliferation as compared to the control (Figure 14A), confirming that leaf-associated WCS417 was at least partially

responsible for triggering IR in *Arabidopsis*. Similarly to a root-dip inoculation, leaf infiltration with WCS417 did not enhance the resistance of *npr1-1* plants to *Pst* (Figure 14 A).

The relative abundance of *Flavobacterium sp.* (ASV4) was significantly enhanced on the leaves of WCS417-treated plants (Figure 13 C). To study a possible new plant immunity-related interaction between the plant and the phyllosphere, I next aimed to test if this bacterium affects defence. As a proxy for *Flavobacterium sp.*, a bacterial strain, Leaf82, from the *At*-LSPHERE collection was utilized (Bai *et al.*, 2015), which displays 100% sequence identity of its V5-V7 16S rRNA gene region with that of ASV4. First, Leaf82 was syringe-infiltrated into leaves of 4-5-week-old *Arabidopsis* plants. Two days later, the same leaves were infiltrated with *Pst*. In contrast to WCS417, local Leaf82 treatment did not reduce *Pst* proliferation on the leaves and thus did not induce local IR (Figure 14 B).

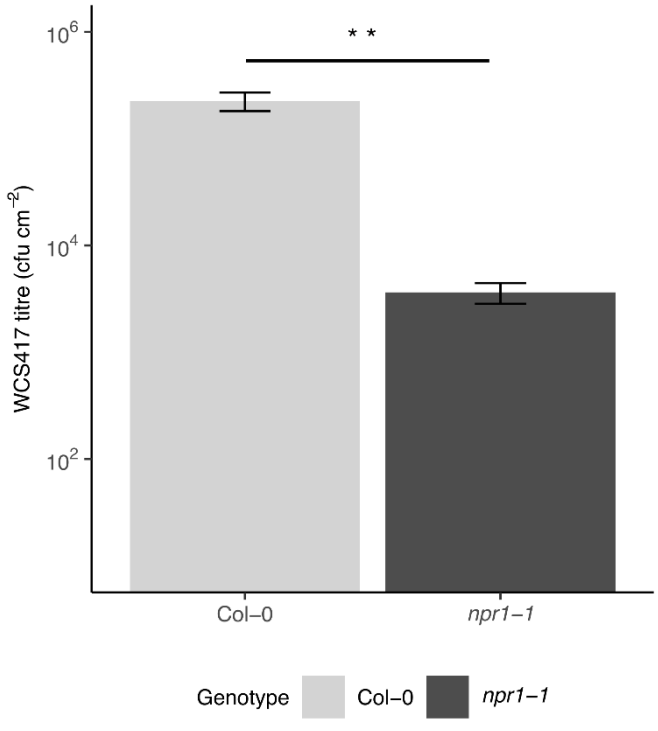


Figure 15: WCS417 titres in Col-0 (wild type) and npr1-1 mutant plants.

*Leaves of 4-5-week-old Arabidopsis plants of the genotypes indicated below the panel were syringe-infiltrated with WCS417. The resulting in planta WCS417 titres are shown at 6 dpi. Bars represent the mean of two biologically independent experiments, including three replicates each ± SE (Student's t-test, **, p <0.01).*

To evaluate whether the proliferation of Leaf82 might affect plant resistance systemically, the first and second true leaves of either wild type or *npr1-1* mutant *Arabidopsis* plants were infiltrated with Leaf82 and the systemic leaves were challenged with *Pst*. As a positive control, *Pst/AvrRpm1* was used for the primary

treatment; as a negative control, the plants were infiltrated with 10mM $MgCl_2$. In wild type plants, *Pst* proliferation was reduced in the systemic tissue of plants undergoing a local *Pst/AvrRpm1* infection as compared to the negative control, indicating a successful SAR response (Figure 14 C). Similarly, a local Leaf82 treatment reduced the propagation of a systemic *Pst* inoculum as compared to the negative control treatment, suggesting the induction of SAR in response to Leaf82 (Figure 14 C). In *npr1* mutant plants, *Pst* titres were similar, irrespective of the treatment, suggesting that Leaf82-induced SAR was abolished in the absence of functional NPR1 (Figure 14 C). Thus, Leaf82 triggers SAR against *Pst* and this response is dependent on *NPR1.* In addition to inducing SAR, Leaf82 also promoted plant growth after a leaf-dip treatment (Figure 16).

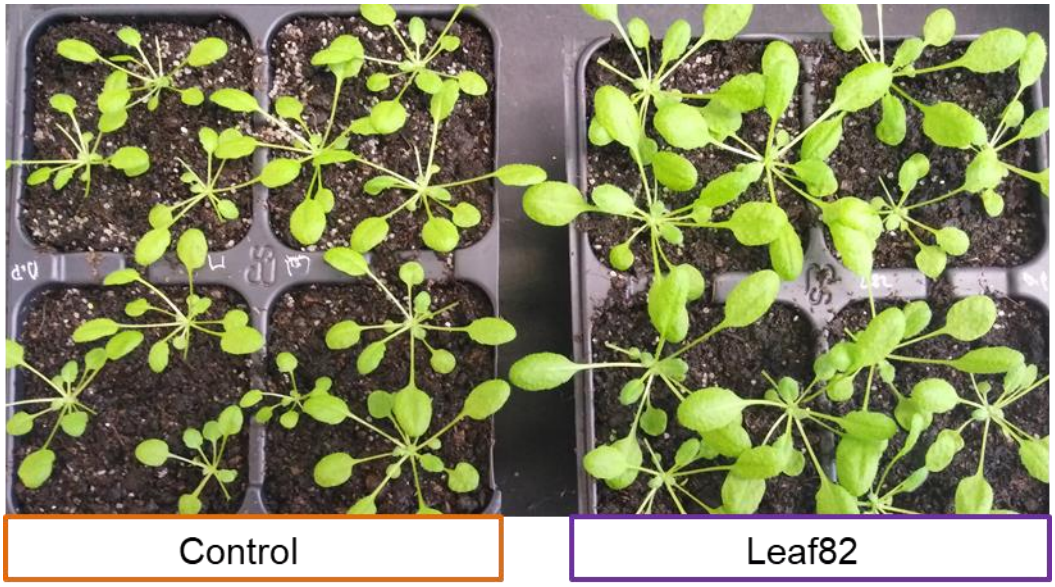


Figure 16: At-LSPHERE Flavobacterium sp. Leaf82 promotes Arabidopsis growth.

The leaves of 10-day-old, sterile-grown seedlings were dip-inoculated with Flavobacterium sp. Leaf82 (OD600 = 0,2 in 10 mM MgCl2) and transferred to soil. The control plants were treated in the same manner except that the Leaf82 bacteria were not added to the inoculum. The picture was taken at 23 dpi. This experiment was repeated twice with comparable results.

4.1.6 Microbe-microbe-host interactions in the Arabidopsis phyllosphere

Finally, I investigated, if WCS417-induced defence responses of *Arabidopsis* influenced the proliferation of *Flavobacterium* sp. during local IR. To this end, the same experiment as above, was performed, and leaves of 4-5-week-old *Arabidopsis* plants were infiltrated with WCS417 or with 10 mM $MgCl_2$ as the negative control. Two days later, the same leaves were infiltrated with Leaf82. Although WCS417-triggered local IR was associated with enhanced proliferation of *Flavobacterium sp.* on the leaves, leaf inoculation of WCS417 did not cause enhanced growth of a subsequent Leaf82 inoculum (Figure 14 D). In contrast, the proliferation of Leaf82 was reduced on WCS417-treated *npr1* mutants as compared to the wild type control (Figure 14 D). Similarly, WCS417 proliferated less on *npr1* mutant than on wild type plants (Figure 15). Thus, the data suggests that WCS417 activates *NPR1*-dependent responses in plants that reduce growth of pathogenic *Pst* and at the same time enhance WCS417 proliferation. Because Leaf82 titres did not appear to be directly regulated by local WCS417 proliferation (Figure 14 D and Figure 10 B) but were reduced on *npr1* mutant plants in the presence of WCS417 (Figure 14 D and Figure 15), the data suggests that *Flavobacterium sp.* is subject to immunity-related plant-microbe-microbe interactions in the phyllosphere.

4.2 IR INDUCED BY *BT*

4.2.1 Bacillus thuringiensis elicits IR at the roots of A. thaliana by means of priming

Bacillus thuringiensis is known to possess growth promoting traits and has been reported to induce IR in tomato plants (Akram et al., 2013). I aimed to test the ability of *B. thuringiensis* (referred to below as *Bt*) to elicit IR in Arabidopsis and to infer on signaling molecules involved in the establishment of this resistance. To induce IR, *A. thaliana* seeds were sterilized and sown on Murashige & Skoog medium. One week later, the sterile-grown *A. thaliana* seedlings were incubated with their roots in the *Bt* suspension or in 10 mM $MgCl_2$ as the control. Afterwards, the seedlings were transferred to soil and propagated in the growth chamber for 3.5 weeks as described above (Wenig *et al.*, 2019). Subsequently, the leaves of the plants were inoculated with *Pst* by syringe infiltration and resulting colonization rates were determined four dpi as described (Wenig et al., 2019). Bacteria grew to significantly lower titres in the leaves of *Bt*-treated compared to control-treated plants, suggesting the establishment of enhanced resistance in *A. thaliana* in response to *Bt* (Figure 17 A).

Since *Bt* has been shown to exhibit antimicrobial properties (Janakiev et al., 2020; Khan et al., 2022), I investigated a possible growth inhibition between *Bt* and *Pst* in a plate-based confrontation assay (Figure 18). The absence of growth inhibition zones in the confrontation assay and the spatial separation of *Bt* and *Pst* on different plant organs (see below) strongly suggest that *Bt*-induced resistance against *Pst* was mediated by plant immune processes. To study plant-mediated responses, leaf tissue from *Bt*- and control-treated plants was harvested 3.5 weeks after the treatment (i.e. before infection, T0) and 2, 4, and 6 hours post-inoculation (hpi). Subsequently, gene expression and possible priming was evaluated utilizing RT-qPCR.

IR to the model PGPR *P. simiae* WCS417 is associated with priming of JA-associated defence genes, including *VEGETATIVE STORAGE PROTEIN1* (*VSP1*) (Pozo et al., 2008; S. van Wees, Luijendijk, Smoorenburg, Loon, & Pieterse, 1999). Here, *Bt*-induced and primed transcriptional responses of *VSP1* as well as of the SA marker gene *PR1* and the SAR marker gene *FMO1* were tested. Similarly to its response to

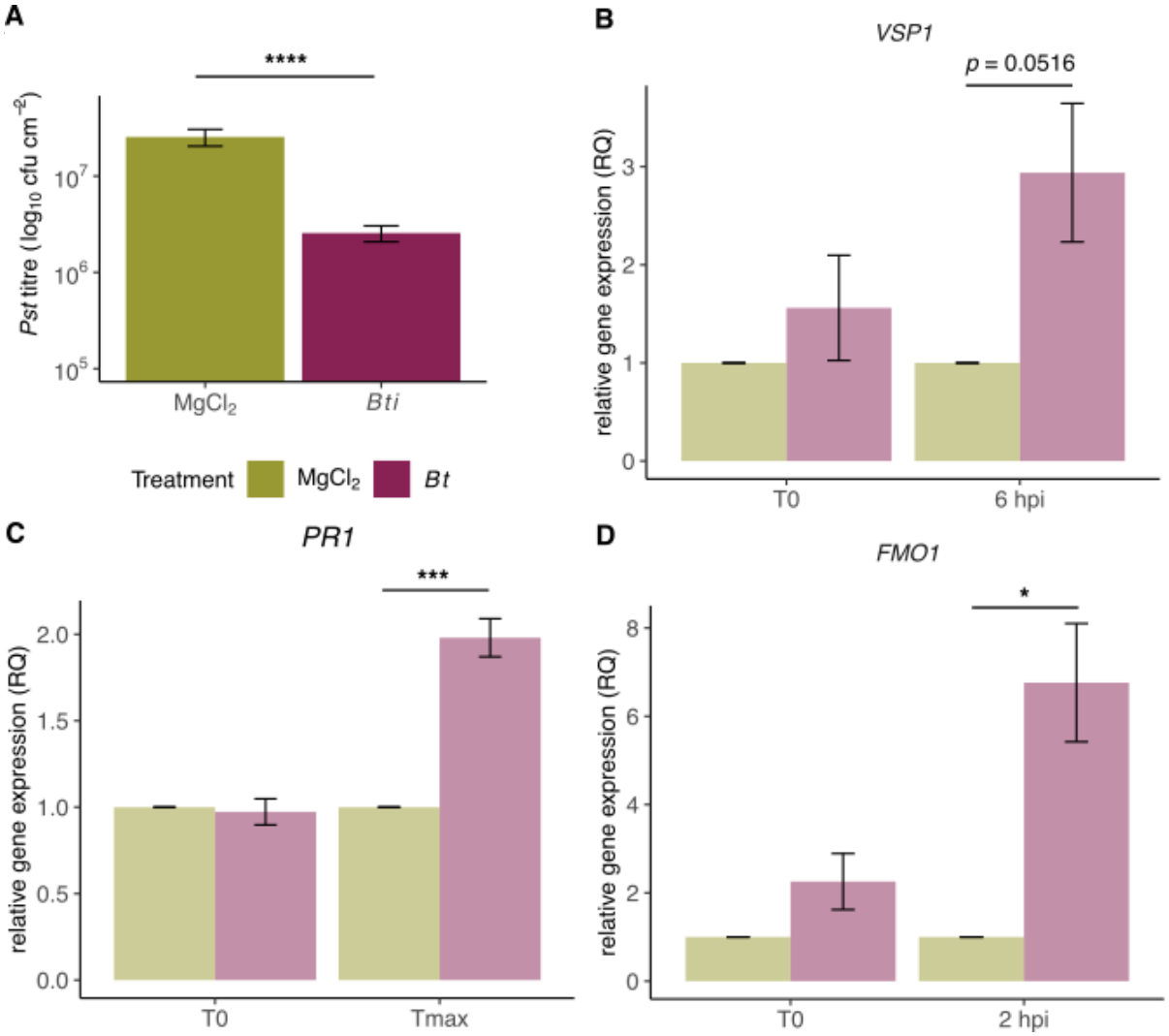


Figure 17: Bacillus thuringiensis (Bt)-triggered induced resistance against Pseudomonas syringae pv tomato (DC3000) in Arabidopsis thaliana is associated with priming.

*The roots of one-week-old sterile-grown seedlings were treated with Bt or a corresponding $MgCl_2$ control treatment and the seedlings subsequently propagated on soil for three weeks. (A) Leaves of the plants were inoculated with DC3000, in planta titres of which were determined at 4 days post-inoculation (dpi). Bars represent average DC3000 titres from three biologically independent experiments, including three replicates each, ± standard error (SE). (B/C/D) Leaves from the treated plants were harvested before infection (T0) and 2-, 4-, and 6-hours post-inoculation (hpi). Transcript accumulation of VSP1 (B), PR1 (C), and FMO1 (D) were determined by RT-qPCR at the time points indicated below the panels. Tmax in (C) indicates a merged analysis of the transcript peaks from 4 and 6 hpi depending on the biologically independent replicate experiment (Supplementary Fig. S2). Transcript accumulation was normalized that of UBIQUITIN and is shown relative to the respective controls. Bars represent average relative transcript accumulation from three biologically independent replicate experiments ± SE. (A-D) Normal distribution of the data was tested and rejected using the Shapiro-Wilk test of normality (P<0.05). Asterisks indicate statistically significant differences between treatment and control (Kruskal-Wallis test, *, P ≤ 0.05, ***, P ≤ 0.001, ****, P ≤ 0.0001). cfu, colony forming units; RQ, relative quantification*

change significantly in response to *Bt* (Figure 17 B, T0). The same was observed for *PR1* and *FMO1* (Figure 17 C/D, T0), suggesting that the JA, SA, and SAR pathways were not directly activated by *Bt.* Considering that IR is associated with priming, in the next step, the transcript accumulation of *VSP1, PR1,* and *FMO1 was* investigated at 2, 4, and 6 hpi (Supplementary Figure 2). Gene expression changes were observed with transcript accumulation peaking at different times after inoculation. *VSP1* transcripts peaked at 6 hpi, displaying a priming trend with a near to significant rise in *Pst*-inoculated, *Bt*-treated as compared to control-treated plants (Figure 17 B). *PR1* transcripts peaked at 4 or 6 hpi; a merged analysis considering the *PR1* transcript peak maximum per biologically independent replicate experiment (T_{max}) suggests that *Bt* primed *PR1* for enhanced transcript accumulation upon *Pst* challenge inoculation (Figure 17 C). Finally, *FMO1* transcripts peaked at 2 hpi, displaying significant priming upon inoculation of *Bt*-treated plants with *Pst* (Figure 17 D). Together, the data suggest that *Bt*-induced resistance relies at least in part on priming of *A. thaliana* defence genes.

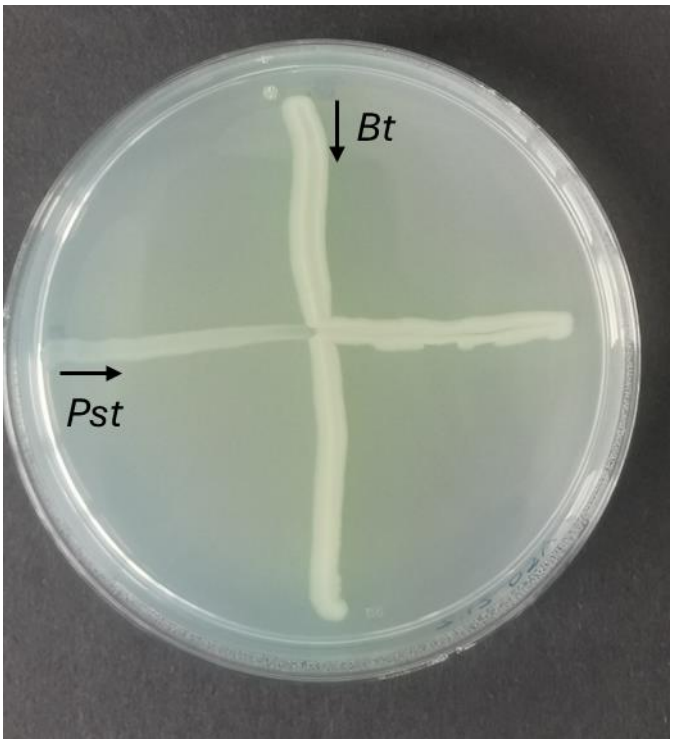


Figure 18: Bacterial interaction assay.

Pseudomonas syringae pathovar tomato (DC3000) and Bacillus thuringiensis (Bt) were streaked crosswise onto an NB-Agar plate and incubated at 25°C for 24 h.

4.2.2 Molecular requirements of IR induction by B. thuringiensis

Next, it was investigated if *Bt*-induced resistance was dependent on functional plant defence responses. Since the JA marker gene *VSP1* displayed a priming tendency, *Bt*-induced resistance in *jasmonic acid resistant1* (*jar1*) mutant plants was tested (Staswick & Tiryaki, 2004). *Bt*-treatment of *jar1* reduced the propagation of a subsequent *Pst* inoculum to a similar extent as in wild type plants (Figure 19 A), indicating that *Bt*-induced resistance was independent of JA. In contrast, both *sid2* and *npr1-1* mutant plants did not mount *Bt*-induced resistance responses (Figure 19 A). Thus, *Bt*-induced resistance in *A. thaliana* depended on functional pathogen-induced SA accumulation and signaling.

Bt-induced resistance was functional in *ald1* mutant plants (Figure 19 B), excluding a causative role of Pip in *Bt*-triggered IR. Since *FMO1*, which encodes the enzyme that converts Pip to its bioactive derivative NHP, was primed in response to *Bt* (Figure 17 D), a possible role of the SAR signaling intermediate LLP1 in *Bt*-triggered IR was investigated. LLP1 promotes SAR downstream of Pip and in parallel with SA in systemic SAR signal perception and/or (Heiko H. Breitenbach et al., 2014; Wenig et al., 2019). Here, *Pst* cfus were comparable in *Bt*-treated compared to control-treated *llp1-1* plants (Figure 19 B), indicating that *Bt*-triggered IR depended on LLP1.

Thus, *Bt*-triggered resistance in *A. thaliana* relies on signaling intermediates of both pathways contributing to SAR with essential contributions of SA and LLP1. Prior studies associated *Bt* IR with elevated SA-induced gene expression in tomato (Hyakumachi et al., 2013; Takahashi et al., 2014). In *A. thaliana*, I detected a possible priming of SA- and SAR-responsive genes in response to *Bt* (Figure 17 C/D). Together, the data suggest that *Bt* enhances the immunity of plants against pathogens via priming dependent on JA, SA, and Pip.

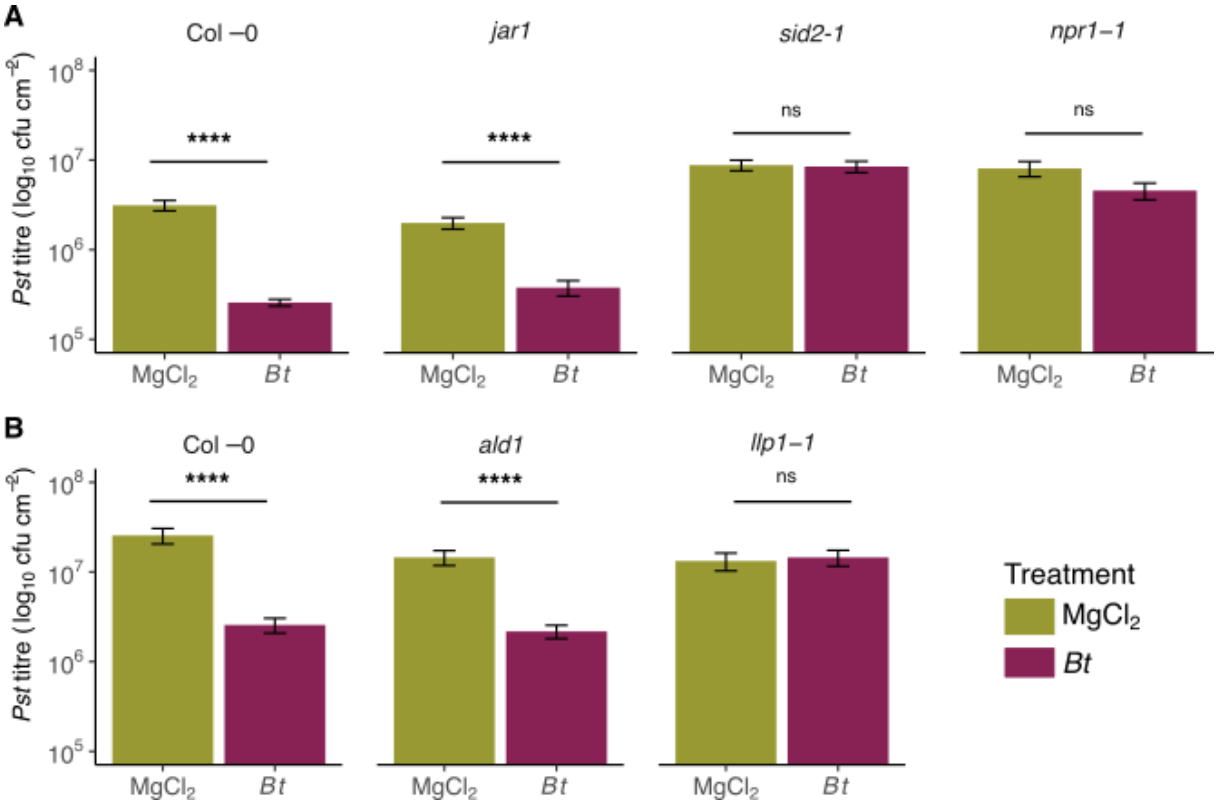


Figure 19: Bt-induced resistance depends on salicylic acid (SA) accumulation and signaling (A) and on the SAR signaling component LEGUME LECTIN-like PROTEIN1 (LLP1) (B).

*(A/B) The roots of one-week-old sterile-grown seedlings of the genotypes indicated above the panels were treated with Bt or a corresponding $MgCl_2$ control treatment and the seedlings subsequently propagated on soil for three weeks. Leaves of the plants were subsequently inoculated with Pst in planta titres of which were determined at 4 dpi. Bars represent average Pst titres from three biologically independent experiments, including three replicates each, ± SE. Normal distribution of the data was tested and rejected using the Shapiro-Wilk test of normality (P<0.05). Asterisks indicate statistically significant differences between treatment and control (Kruskal-Wallis test, ****, P ≤ 0.0001). ns, not significant*

4.2.3 B. thuringiensis can trigger SAR if applied to the leaves

In *A. thaliana*, SAR can be induced by a local inoculation with avirulent *Pst* (Cameron, Dixon, & Lamb, 2004; Wenig et al., 2019). Here, the first two true leaves of 4–5-week-old plants were inoculated with *Bt* or with *Pst* carrying the effector *AvrRpm1* (*Pst/AvrRpm1*) as a positive or 10 mM $MgCl_2$ as a negative control. In contrast to *Pst/AvrRpm1*, which grew to appreciable titres in inoculated leaves, *Bt* survived but did not propagate in *A. thaliana* leaves (Figure 20 A). Three days after the primary treatment, challenge inoculations with *Pst* were performed in the third and fourth leaf of the plants and resulting *Pst* cfus were determined as described (Wenig *et al.*, 2019).

As expected, *Pst* titres were reduced in *Pst/AvrRpm1*-treated plants as compared to the $MgCl_2$ control (Figure 20 B), indicating the establishment of SAR. Similarly, the local treatment with *Bt* reduced propagation of the *Pst* challenge inoculum, suggesting the establishment of SAR in response to *Bt.* Thus, *Bt* triggers SAR-like systemic resistance when applied to the leaves of *A. thaliana.*

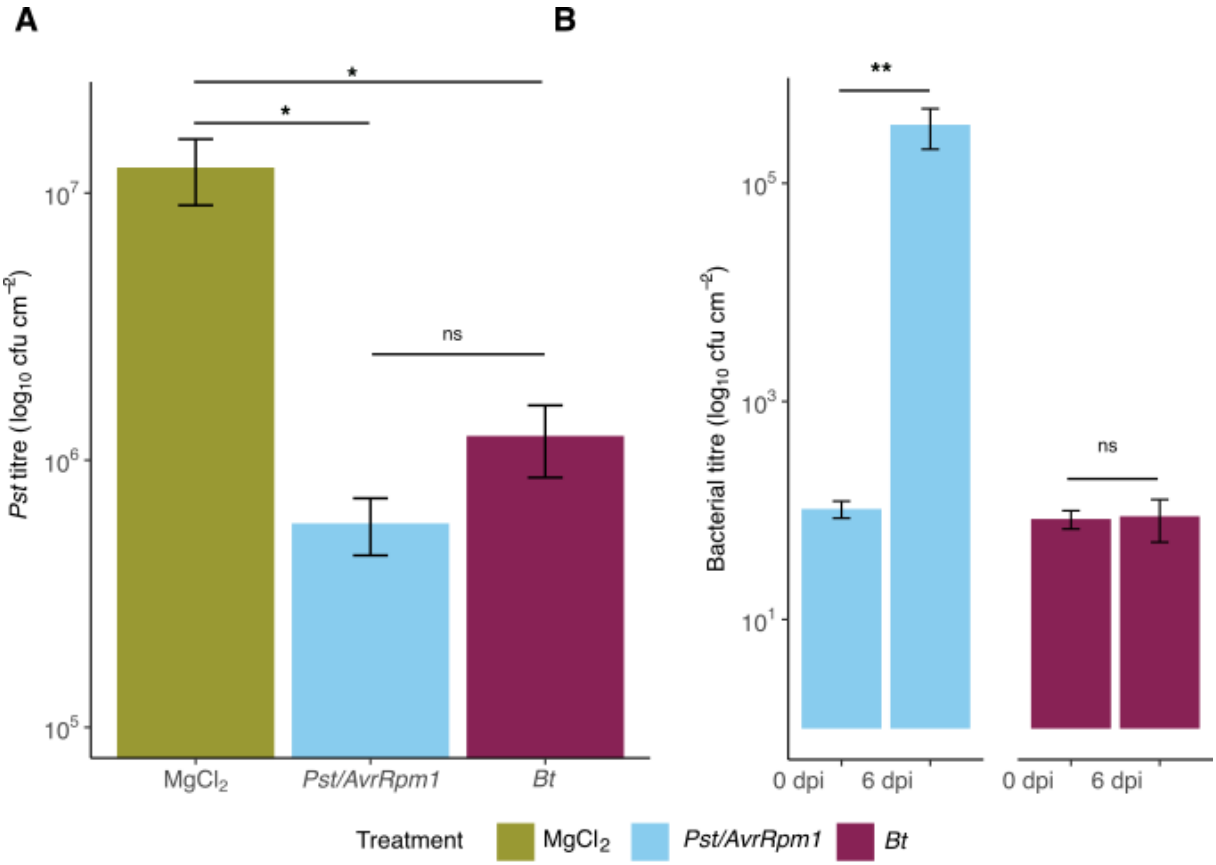


Figure 20: Bt triggers systemic acquired resistance (SAR) in A. thaliana.

*(A) Propagation of SAR-inducing bacteria in A. thaliana leaves. Leaves of 4.5-week-old plants were infiltrated with 10^5 colony forming units (cfu) mL^{-1} of Pst carrying the effector AvrRpm1 (Pst/AvrRpm1; blue bars) or with Bt (magenta bars). The leaf-associated bacterial titres were determined at 2 hpi (0 dpi) and 6 dpi. Bars represent the average of two biologically independent replicate experiments, including three replicates each, ± SE. (B) SAR in A. thaliana. 4.5-week-old plants were infiltrated in their first two true leaves with 10^6 cfu mL^{-1} of Bt or Pst/AvrRpm1 as the positive control or with 10 mM $MgCl_2$ as the negative control. Three days later, the third and fourth leaves of the treated plants were inoculated with 10^5 cfu mL^{-1} of Pst, in planta titres of which were determined at 4 dpi. Bars represent average Pst titres from three biologically independent experiments, including three replicates each, ± SE. (A/B) Asterisks indicate statistically significant differences. Normal distribution of the data was tested using the Shapiro-Wilk test of normality (P<0.05). A) Asterisks indicate statistically significant differences between treatment and control (paired t test, **, P ≤ 0.01). B) Asterisks indicate statistically significant differences between treatment and control (Kruskal-Wallis test, *, P≤0.05; **, P≤0.01). ns, not significant*

4.2.4 *IR triggered by B. thuringiensis does not lead to extensive shifts in the phyllosphere microbiome*

While emerging evidence suggests that the plant immune system influences the composition of the plant-associated microbiota (Bodenhausen et al., 2014; T. Chen et al., 2020; Pfeilmeier et al., 2021; Pfeilmeier et al., 2024; Sohrabi et al., 2023), it is not known whether induced resistance responses, including IR and SAR, have a similar effect. To address these questions, amplicon sequencing on the 16S rRNA gene of the phyllosphere microbiome was performed. So, leaves from 10 plants per treatment were harvested and pooled, 3.5 weeks after inoculation of the plants with *Bt* or 10 mM $MgCl_2$ (control); replicate samples were taken from seven biologically independent experiments. Amplicons derived from PCR were size separated by agarose gel electrophoresis to remove chloroplast derived sequences, which have a higher number of nucleotides. Finally, the three PCR replicates per sample were pooled at equimolar amounts. Indexing and paired-end amplicon sequencing was performed. Subsequent data preprocessing and assignment of bacterial taxa based on ASV utilizing the Silva database ensued. In total, 798 taxa hast been assigned across 14 samples, with an average of 236 ASVs per sample (Yilmaz et al., 2013) .

After removal of ASV1 (a putative chloroplast DNA contaminant) a rarefaction curve was plotted, revealing a sufficient sequencing depth in all samples (Figure 21). Two samples were identified as outliers according to visual inspection of the rarefaction curves as well as by performing a Grubb's test (Grubbs, 1950) on the number of unique ASVs per sample (p <0.005 for control-treated replicate No. 2 and p < 0.05 for *Bt*-treated replicate No.5, Figure 21). The respective data sets were excluded from further analyses. Analysis of alpha diversity in the form of Shannon's and Simpson's Index as well as the absolute numbers of found ASVs per sample did not indicate any significant differences between the treatments (Figure 22)

To infer on the overall impact of the IR treatment on the leaf microbiome, a principal component analysis was performed on log-transformed and variance-stabilized ASV counts. I did not detect significant differences in the overall microbiome composition in the phyllosphere of *Bt*- as compared to control-treated plants (p=0.287) (Figure 23A). Thus, although resistance against pathogens was enhanced, *Bt*-triggered immune

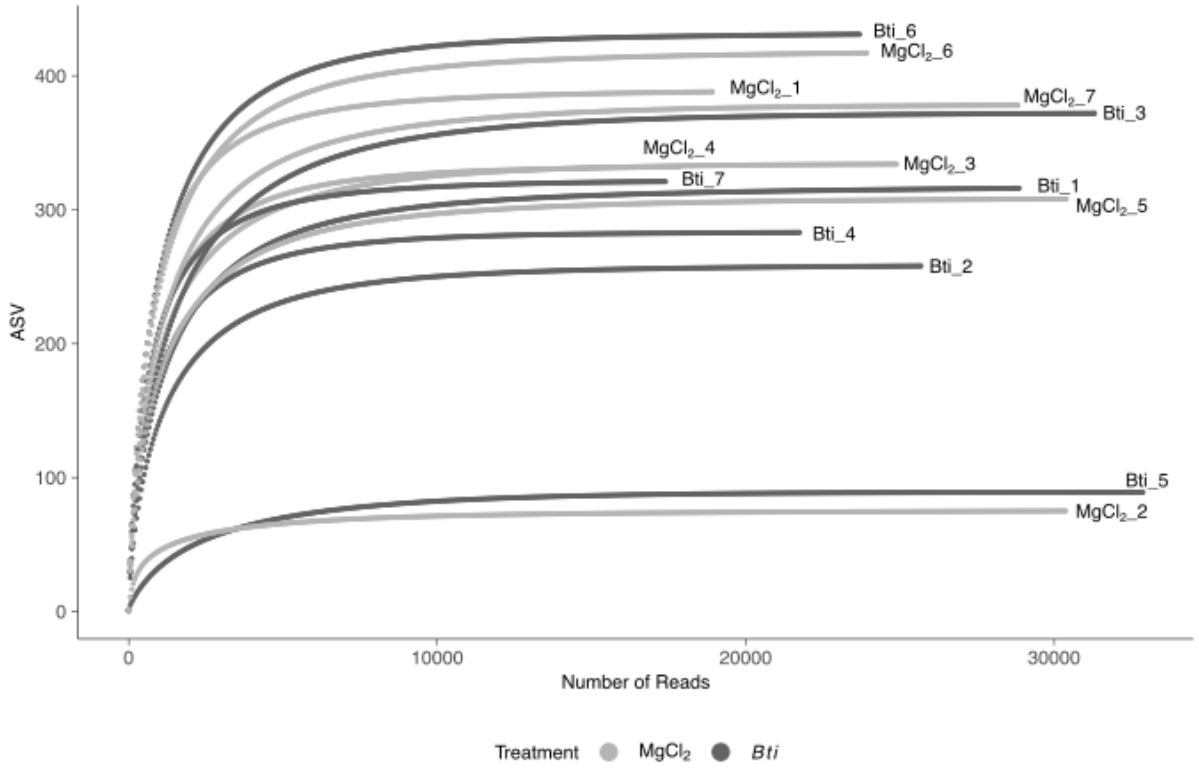


Figure 21: Rarefaction curve of Amplicon Sequencing.

Number of unique Amplicon Sequence Variants (ASV) after amplicon sequencing of leaf material harvested 3.5 weeks after treatment of the plants with Bt or with 10mM MgCl2 (control). Curves represent data from six biologically independent replicate experiments, including pooled leaf material from 10 plants per treatment and replicate. Light grey curves represent samples from MgCl2-treated plants, dark grey lines represent samples from Bt-treated plants. The Y-axis represents Number of unique ASVs sequenced, the x-axis represents the corresponding number of total sequenced reads.

responses in the phyllosphere were not associated with a significant shift in the leaf-associated bacterial microbiota.

Next, I monitored the occurrence of the IR-eliciting *Bt* strain in the leaves by blasting all ASV sequences that were assigned to *Bt*. One ASV exhibited 100% sequence identity with *Bt*. This strain occurred in one sample per treatment with a rate of 0.03% and 0.1% of total reads per sample in *Bt*- and control-treated plants, respectively (Figure 23 B). Whereas I cannot exclude a possible treatment-induced contamination of the phyllosphere with *Bt* in one out of six replicate experiments, the phyllosphere remained free of *Bt* in the other replicates. These findings confirm that *Bt*-induced resistance is most likely established as IR with *Bt* triggering plant-mediated processes in the root, which lead to the establishment of IR in the phyllosphere.

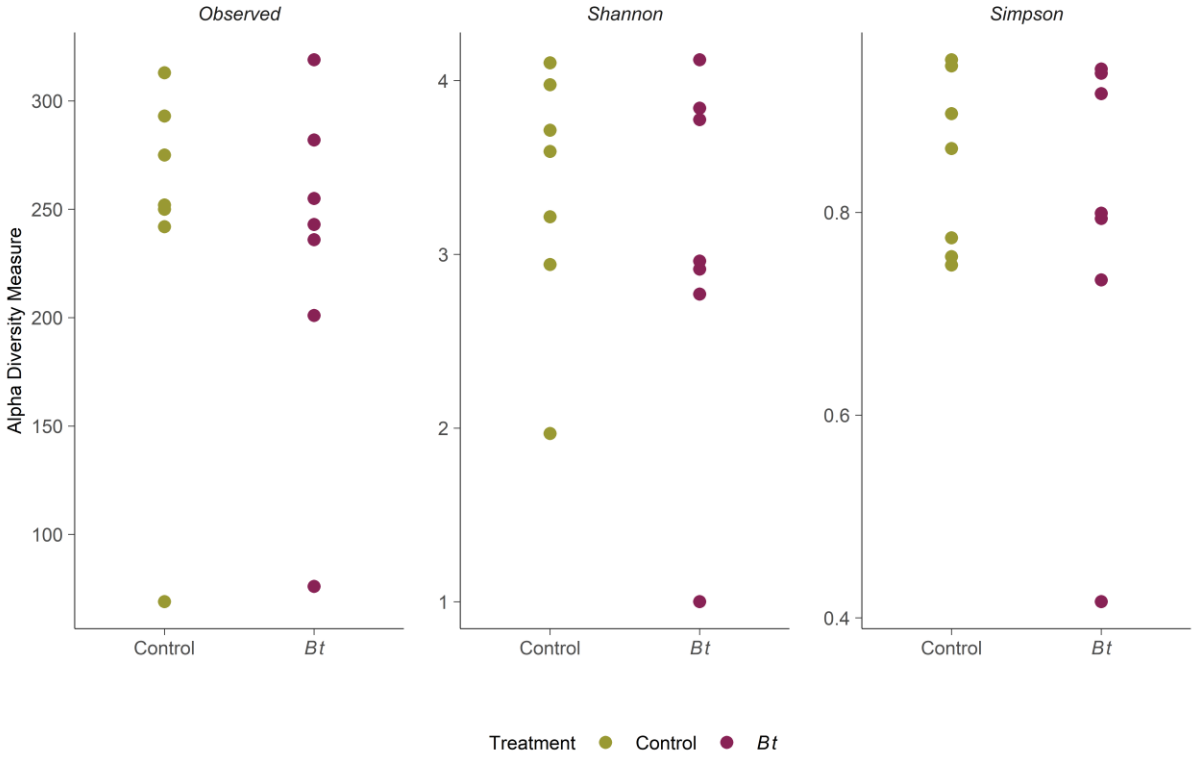


Figure 22: Differences in the microbiome of the phyllosphere following Bt IR treatment in comparison to control-treated plants.

*Leaves of plants grown for 3.5 weeks on soil after root-dip inoculation with either 10 mM $MgCl_2$ (control treatment, green dots) or Bt (red dots) were harvested and amplicon sequencing of the 16S rRNA gene was performed. α-diversity indices of phyllosphere microbiome following Bt- or control-treatment: Number of observed ASVs (left) Shannon's Index (middle) and Simpson's Index (right). The y-axis represents the respective index value, and dots indicate the values of individual samples. Samples from WCS417-treated plants have significantly lower ASV-numbers as well as α-diversity indices than control-treated plants (pairwise t-test, *, p <0.05, **, p < 0.01).*

To gain insight into possible microbial changes on the level of bacterial genera, I searched for significant changes in the number of ASV counts by utilizing DESeq2 (Love, 2014; Pfeilmeier et al., 2021). I detected a near-significant difference in abundance of the bacterial genus *Solimonas* (FDR-controlled *p* value = 0.066) with a log_2-fold change of 11.8 in *Bt*- as compared to control-treated plants (Figure 23 C). This bacterial strain was present in four out of six samples originating from *Bt*-treated plants with abundances varying between 0.2 and 6% of reads per sample. In control-treated plants, one sample contained the respective bacterial strain at an abundance of 0.5% of all reads.

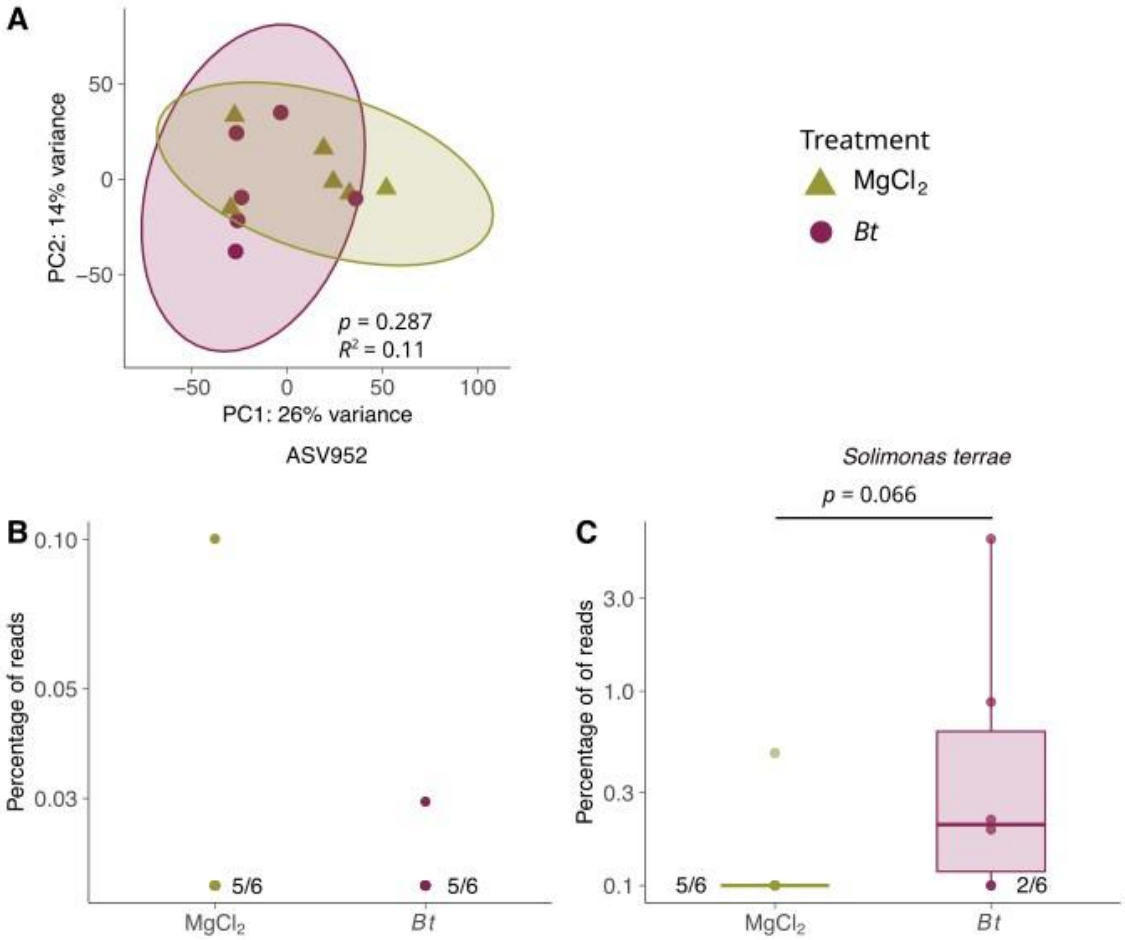


Figure 23: The phyllosphere microbiome is stable under Bt-triggered IR.

The roots of one-week-old sterile-grown seedlings were treated with Bt or a corresponding MgCl2 control treatment and the seedlings subsequently propagated on soil for three weeks. Subsequently, leaves were sampled, and the leaf-associated microbiome evaluated using amplicon sequencing of the bacterial 16S rRNA gene. (A) Principal component analysis of the amplicon sequence variant (ASV) counts as a proxy for microbiome composition in Bt- and control-treated plants. The analysis included data from six biologically independent replicate experiments. Significant differences were excluded by performing a Manova on the distance matrix of the PCA. (B) Relative abundance of ASV952 corresponding to Bt in the phyllosphere of MgCl2- and Bt-treated plants as indicated below the panel. Dots indicate individual data points from biologically independent replicate experiments. (C) Relative abundance of ASV45 corresponding to Solimonas terrae in the phyllosphere of MgCl2- and Bt-treated plants as indicated below the panel. Boxplots indicate average relative abundances of sequenced reads from five biologically independent replicate experiments ± min and max values, points indicate relative abundance per sample. Numbers at the bottom of the graph indicate number of samples without any reads of the respective ASV/total number of samples. Significant differences were excluded using the DESeq2 built in Wald-test, corrected for multiple testing using the Benjamini Hochberg procedure. (B/C)

5. DISCUSSION

In contrast to most vertebrate animals such as us humans, plants can and do regrow organs on a regular basis. Thus, tissue and even organ destruction by pathogenic microbes is not a major threat *per se*. The actual threat arises if the local infection spreads to systemic tissues and the whole plant is getting affected. So, plants have evolved elaborate mechanisms to contain local infections and reduce the risks of systemic involvement. One of those mechanisms is the triggering of systemic immunities like PGPR/F IR and SAR, which aim to prevent and contain systemic infections. In this thesis, I aimed to enhance our understanding of this process. To do so, I traced the establishment of PGPR IR from the bacteria at the roots throughout the whole plant towards the bacteria in the leaves; in other words, towards the microbiome of the phyllosphere.

And so, this journey begins at the roots…

5.1 BACTERIAL ELICITATION OF IR

One aim of this work was to evaluate if *Bacillus thuringiensis* (*Bt*) elicits an induced resistance when applied to the roots of *Arabidopsis thaliana*. In the past, many studies have been conducted on the disease-protective and plant growth-promoting properties of members of the genus *Bacillus* (Serrão, Ortega, Rodrigues, & de Souza, 2024; Soni & Keharia, 2021; N. Zhang et al., 2023). Members of this genus are gram-positive, rod-shaped bacteria with the capability to form endospores (Weber & Rutala, 1988). Those spores are able to outlive very harsh conditions for very long periods of time while being in a dormant state. This capacity makes them ideal candidates for root treatments, since they can persist in the soil throughout droughts, seasonal changes and unfavourable conditions (Setlow, 2014). Furthermore, *Bacillus* spp. are known for their broad range of secondary metabolites with a plethora of functions, among them antimicrobial properties. They are able to secrete those antimicrobial compounds into

their environment. One strain of *B. amyloliquefaciens* for example has been reported to have ~10% of its genes coding for antimicrobial compounds (S. P. Chowdhury, Hartmann, Gao, & Borriss, 2015).

Another type of secreted secondary metabolites are extracellular polymeric substances (EPS), which are the construction material for biofilms. The capacity to form biofilms is another asset in colonizing and persisting in the rhizosphere of plants, since they form a three-dimensional habitat for complex microbial communities (Flemming & Wingender, 2010). Additionally, they offer protection from different environmental factors like desiccation, antimicrobial compounds or physical dislocation, for example, by rain (Arnaouteli, Bamford, Stanley-Wall, & Kovács Á, 2021; Costerton, Lewandowski, Caldwell, Korber, & Lappin-Scott, 1995). Thus, the capacity to form biofilms offers an advantage in the colonization of root surfaces and help outcompete potential pathogenic strains (Costerton et al., 1995).

A lot of microbes which seemed to be very promising IR candidates in the very controlled conditions of a scientific lab showed highly varying levels of protection and persistence in field trials (Burpee, 2009; Paulitz & Bélanger, 2001). Finding good and persistent root colonizers for the induction of IR is an integral part in bringing the science from the bench onto the fields. Several studies were able to show that high numbers of beneficial microbes in the rhizosphere correlates to better plant protective properties efficacies (Annapurna et al., 2013; Gopireddy, Devi, Kumar, Babu, & Naidu, 2018; T. Müller & Behrendt, 2021).

The plant protective traits granted by *Bacillus* spp. manifest in a three-fold way: On the one hand, they act directly antagonistically towards pathogens. This is achieved by competing for resources and producing antimicrobial compounds such as antibiotics, cell wall-degrading enzymes, chitinases and VOCs. (G. S. Jouzani, Valijanian, & Sharafi, 2017; Nazari & Smith, 2020). However, I could not find any direct antagonism of *Bt* against *Pst* in a plate-based interaction assay. Another strategy to inhibit growth of potential pathogens is interference with quorum sensing (QS): Bacteria interact with each other by releasing certain communication molecules into their environment. This QS called communication is important for synchronizing processes in larger groups of cells. It can help for example in biofilm formation or triggers bioluminescence in *Vibrio fisheri* to commence only at certain cell densities (Dickschat, 2010; Nealson & Hastings, 1979). In facultative pathogenic bacteria like *Staphylococcus aureus*, it is

utilized to switch lifestyle from commensal to pathogenic after reaching a certain threshold of cell density (Mukherjee & Bassler, 2019; Waters & Bassler, 2005). By releasing enzymes which degrade such signaling molecules and by thus interfering with this communication, some microbes can disturb various bacterial adaption mechanisms like biofilm formation, production of compounds with antibiotic properties, or rendering some pathogens non-infectious. (Y. H. Dong, Zhang, Xu, & Zhang, 2004).

The second way, *Bacillus* spp. can protect plants is to improve the plant's overall fitness by improving e.g. nutrient uptake or root architecture. *Bt* has been reported to be an auxin-producer and to secrete phosphate-solubilizing molecules (G. S. Jouzani et al., 2017). Additionally, it can increase the activity of antioxidant enzymes, thus reducing oxidative stress (Armada, Probanza, Roldán, & Azcón, 2016). *Bt* has further been shown to increase overall plant fitness during drought stress. This makes it an interesting target in the upcoming challenges resulting from climate change (Armada, Azcón, López-Castillo, Calvo-Polanco, & Ruiz-Lozano, 2015; Ortiz, Armada, Duque, Roldán, & Azcón, 2015).

The third mode of plant protection by *Bacillus* spp., and of most interest in this treatise, is the ability to trigger a systemic resistance when applied to the roots of the plants. Serrao and colleagues recently published a meta-study on *Bacillus* spp. as tools for biocontrol of plant diseases and analysed the study data of the last 20 years. They found that *Bacillus* spp., if used as biocontrol agent, was able to reduce disease severity on average by ~60%. They manage this either in direct microbe-microbe interactions or by eliciting plant immunity responses. In this meta-study, it is remarkable that out of >5000 studies, only two focused on *Bacillus thuringiensis*, which emphasizes the motivation of this work, to broaden our knowledge of the biocontrol properties of *Bt* (Serrão et al., 2024). This *Bacillus* species is not just one more in the already extensive collection of PGPRs. It brings the additional benefit of insecticidal proteins, the CRY proteins (Bravo, Gill, & Soberón, 2007). Those affect mainly insects and even some nematodes and parasitiformes, depending on the variety of CRY protein (Iatsenko, Boichenko, & Sommer, 2014; Iatsenko, Corton, Pickard, Dougan, & Sommer, 2014; Gholamreza Salehi Jouzani et al., 2008). Those proteins became famous for the development of the so-called BT-plants like maize, cotton of even aspens which are more resistant against insect feeding (Ibrahim & Shawer, 2014). Each variety of CRY protein targets usually a specific, very narrow range of species (Jurat-Fuentes & Crickmore, 2017). Since the genes coding for CRY proteins are often

localized on plasmids (Reyes-Ramírez & Ibarra Jorge, 2008), it is even possible to engineer a *Bt* strain to specifically cater to any specific needs of insect- or nematode reduction while at the same time enhancing the plant's immunity towards pathogenic microbes and thus enhancing the overall plant's health on a very broad scale. To further this goal, I was able to show that *Bt* is capable of eliciting PGPR IR in Arabidopsis (Figure 17). Leaf infiltration of *Pst* following *Bt* root-dip treatment led to less proliferation than in control-treated plants. Since I could show that *Bt* does not interfere with *Pst* growth on Agar plates and *Bt* is not enriched in the phyllosphere, I can conclude that the heightened resistance of Arabidopsis is indeed due to IR induction and not due to direct microbe-microbe interactions.

However, for the sake of completeness, it is prudent to mention possible pitfalls in this setup: *Bt* is closely related to *B. cereus* and *B. anthracis*. Both bacterial species are known to cause diseases in humans and are known to find reservoirs in plants (Ganz et al., 2014; Stenfors Arnesen, Fagerlund, & Granum, 2008). Since many of the virulence factors *B. cereus* and *B. anthracis* are located on plasmids and thus can be transferred onto otherwise beneficial *Bt* strains, this might pose a potential risk to human health (Adams et al., 2014). This risk needs to be evaluated carefully before putting *Bt* to use in agriculture.

In contrast to *Bt*, WCS417 is capable of synthesizing only a very limited range of antimicrobial agents and thus cannot supress the proliferation of pathogenic microbes in the rhizosphere via direct antagonism (C. M. J. Pieterse et al., 2021).

This fits very well with my own observations of WCS417 not restraining *Pst* growth in an agar-plate based interaction assay. However, WCS417 can still outcompete potential pathogens in the fight for nutrients like iron in the nutrient-limited soil and rhizosphere environment. In fact, the original specific epithet "*fluorescens"* was given for the ability of WCS417 to excrete fluorescent siderophores for iron scavenging (Figure 24) (C. M. J. Pieterse et al., 2021). WCS417 was renamed 2015 to *Pseudomonas simiae.* This was done, since sequencing revealed 100% sequence identity with the beneficial *P. simiae* strain R81, which has been isolated from wheat roots in India due to its plant protective properties (Berendsen et al., 2015; Mathimaran, Srivastava, Wiemken, Sharma, & Boller, 2012).

Similar to *Bt*, WCS417 is a very good colonizer of plant roots. In general, *P. fluorescens* strains have been shown to be excellent colonizers of the rhizosphre and thus to be highly enriched there (P. A. Bakker, Berendsen, Doornbos, Wintermans, & Pieterse, 2013). The question arises then, how PGPR evade the plant immune response, i.e. the perception of MAMPS, which PGPR introduce to the plant's environment. Those should elicit a comparable PTI response which is also triggered by MAMPs on pathogens and helps fend off pathogenic microorganisms. For WCS417, this question is at least in part resolved: WCS417 can reduce the rhizosphere pH in its immediate surroundings by exuding gluconic acid and 2-keto gluconic acid. This acidification appears to suffice to restrain rhizospheric immune responses (Ke Yu, Liu, et al., 2019;

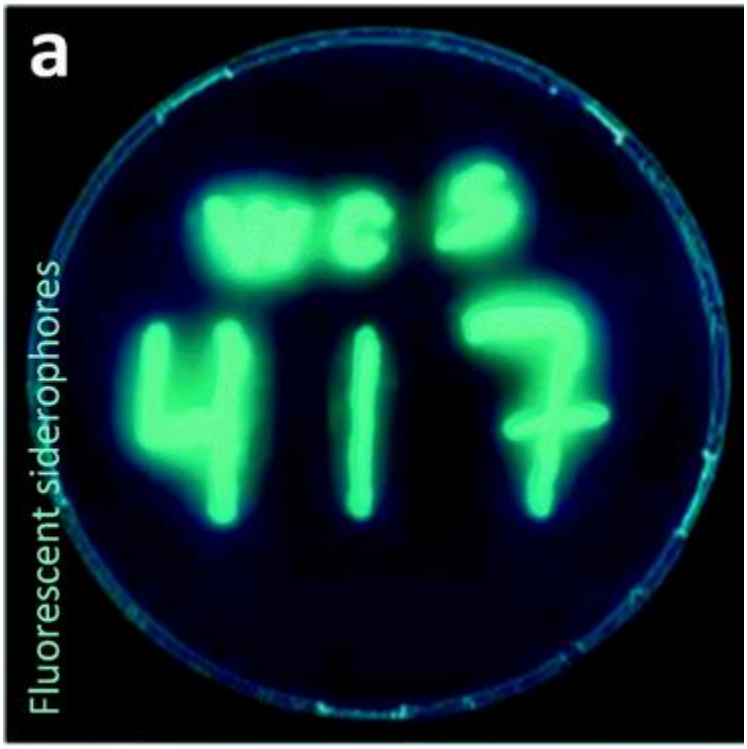


Figure 24: WCS417 producing a fluorescent pyoverdine siderophores on culture medium with low iron availability.

Adapted from Pieterse et al, 2021

Ke Yu, Pieterse, Bakker, & Berendsen, 2019). This evasion of the plant's immune response is pivotal to the colonization of the rhizosphere with beneficial microbes (Santoyo, Urtis-Flores, Loeza-Lara, Orozco-Mosqueda, & Glick, 2021).

In concordance to these findings, WCS417 adhered to and proliferated in the rhizosphere of Arabidopsis plants in the root-dip assay I deployed in this work (Figure 7).

Further experiments showed that WCS417was not only capable of proliferating in the rhizosphere, but of also of reaching and proliferating in the phyllosphere. There, it did

prime a local IR against *Pst*. This is in contrast to classical IR as has been found after soil-drench treatment by Pieterse and colleagues, which is initiated at the roots and then takes effect in the whole plant (C M Pieterse et al., 1996).

5.2 Signal transduction of PGPR IR in planta

The journey of PGPR IR throughout the plant has started: the interaction of bacteria with the plant has set a signal cascade into motion, which will affect the whole plant and will enhance the state of resistance up to the very tips of the leaves.

To this day, it is not entirely clear, how the signal that derives from bacteria or fungi to elicit IR, is perceived and then relayed throughout the plant up to the leaves. It is known that this signaling mechanism can differ between different eliciting microbes (A. C. Vlot et al., 2020). It is important to distinguish between different contexts (before or after pathogenic challenge) and different plant organs (root vs. shoot), when reporting IR manifestation by changes in gene transcript accumulation. It is known that gene expression patterns are subject to dynamic changes depending on these parameters, e.g. rapid changes in gene expression after pathogen encounter (Uwe Conrath et al., 2015; Martinez-Medina et al., 2016).

5.2.1 IR signal transduction in Bt IR

To elucidate the signaling pathways involved in *Bt* IR, I analysed transcriptional changes in the leaves of *Bt*-treated plants after IR treatment, but before pathogenic infection and additionally at short time intervals post infection. Furthermore, loss-of-function mutants were utilised to inquire about signaling dependencies in IR transmission.

PGPR/F IR often depends on priming, which means that the plant does not directly increase its gene expression upon contact to PGPR/F. Instead, there are more subtle, often epigenetic changes, which lead to a faster and stronger response after contact to pathogens in comparison to naïve plants without previous contact to PGPR/F (Martinez-Medina et al., 2016). Before the infection, however, the respective gene expression is not higher than in control-treated plants.

For WCS417, this phenomenon was known and already described in previous literature (S. van Wees et al., 1999). Here I could show that the gene expression of *PR1* in *Bt* treated plants reached a peak 2h-6h after *Pst* induced pathogenic challenge, which is significantly higher than in naïve control-treated plants. Thus, *PR1* can be considered as primed. Additionally, *Bt* IR resistance was abolished in *sid2-1* mutants. Thus, I can conclude that *Bt* IR is depended on SA signaling components. Hyakumachi and colleagues also found evidence for SA dependent signaling after *Bt* IR in tomatoes: If the roots were treated with *Bt* serovar *sotto* RG1 and then consecutively were infected with *R. solanacearum*, transcript accumulation of *PR1* increased 48 hpi. However, in this study, the transcript accumulation of *PR1* also increased directly after IR treatment, independent of a pathogenic challenge. Thus, these authors did not necessarily describe a form of priming but rather a direct induction of defence gene expression after *Bt* treatment (Hyakumachi et al., 2013). These discrepancies between their findings and mine might be rooted in the different plant organs infected (root in contrast to leaf) and in the different timepoints of sampling: 48h hours after *Bt* treatment in contrast to 24 days of treatment. This would also concur with results from Wang et al, who elicited IR with *Bt* strain 4F5 in *Brassica campestris*. They found an induction of marker genes for SA signaling (*BnWRKY70)* and JA signaling (*BnHel* and *BnPDF1.2)*. *BnWRKY70* transcript accumulation peaked at 5 days post treatment (dpt) and was almost back to basal levels at 7dpt. *BnHel* transcript levels peaked at 2dpt and returned to a basal level at 5dpt. *BnPDF1.2* were still rising at 7 dpt though (Figure 25) (M. Wang et al., 2020). Thus, transcript levels of some of the marker genes evaluated peaked 2-5 days after IR treatment and restored basal transcript levels shortly after. Thus, there might be a short period of time of direct gene induction after the IR treatment, which is followed by a primed plant response without elevated transcript accumulation in systemic tissues. Since I tested transcript accumulation 24 days past IR treatment, I might have recorded the primed gene responses, whereas Wang and Hyakumachi might have observed the direct induction of gene expression directly post IR treatment.

Another possible explanation for the priming of gene expression in contrast to direct induction is of course, that the cited experiments were performed in tomato plants or *B. campestris*, whereas I utilized the model plant Arabidopsis. Another example of direct induction of changes in gene expression and subsequent accumulation of secondary metabolites is a study performed by Akram and colleagues. They found

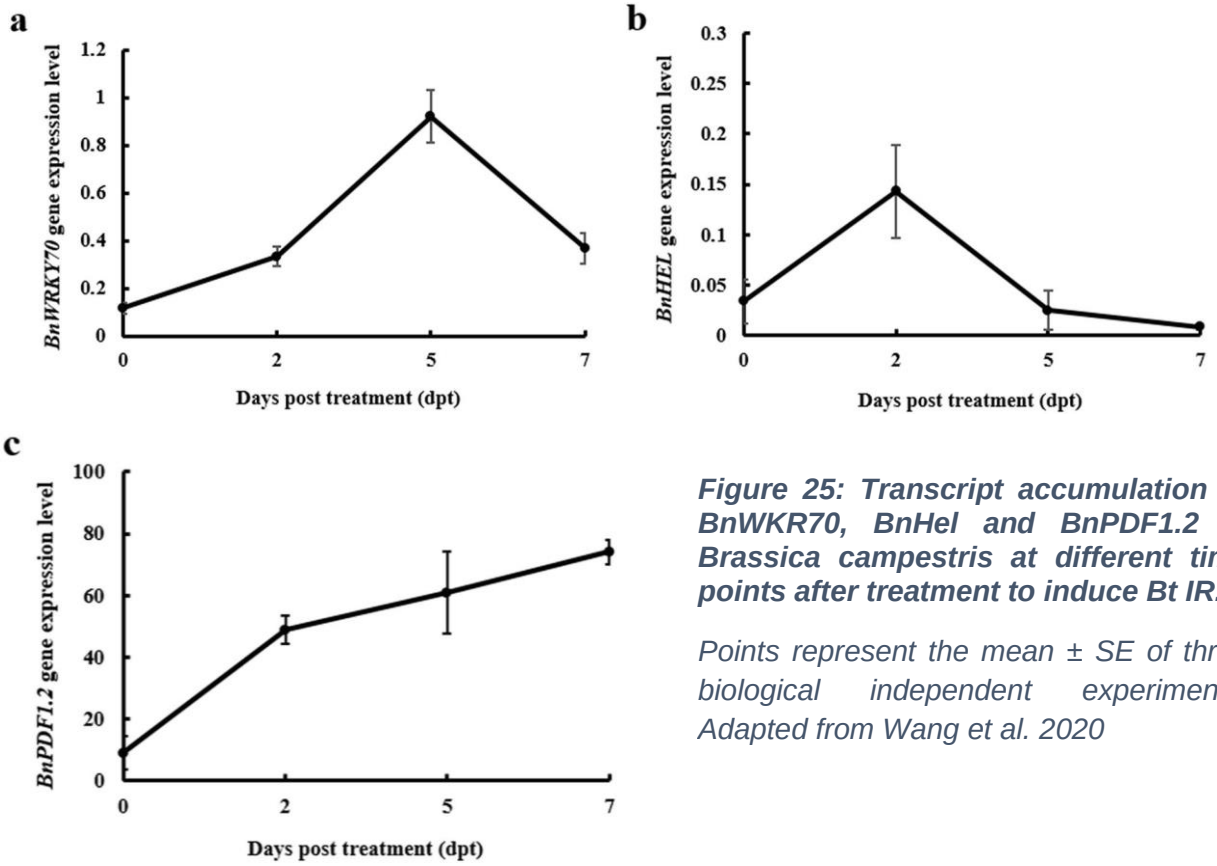


Figure 25: Transcript accumulation of BnWKR70, BnHel and BnPDF1.2 in Brassica campestris at different time points after treatment to induce Bt IR.

Points represent the mean ± SE of three biological independent experiments. Adapted from Wang et al. 2020

significant changes in phenolic contents in tomato treated with *Bt* strain 199, which is also able to elicit IR in tomato. Those changes in phenolic contents were reinforced if the plant was infected with *Fusarium oxysporum* at the same time as the IR treatment. However, increase in phenolic compounds and pathogenicity associated enzymes like PAL were also found independent of a pathogenic challenge (Akram et al., 2013). PAL incidentally is an enzyme which promotes an important step in the SA biosynthesis, which again points to my finding of an SA dependency in *Bt* IR signaling (C. Vlot et al., 2009).

Pip is another signaling component, which might play an ancillary role in IR-dependent signaling (add citations, general role!). I initially believed that it might play a role in *Bt*-IR, since *FMO1* gene expression increased after pathogenic infection of *Bt*-treated plants in a similar manner as *PR1*. However, since plants unable to synthesize Pip (namely: *ald1* mutants) still were able to mount an IR similar to that of Col-0 wt, Pip does not appear to be required for a successful establishment of *Bt* IR. The priming of *FMO1* might be part of the SA-Pip self-enforcing regulatory loop dependent on SARD1/CBP60g and NPR1 (C. Vlot et al., 2021). And indeed, *Bt* IR is dependent on functional NPR1, which was shown by the missing IR induction in *npr1-1* mutants. Yet, functional NPR1 is also a precondition not only for SA signaling, but also for JA-

dependent IR (Nie et al., 2017). Thus, the role of NPR1 is not fully elucidated in PGPR IR at this point.

Bt IR showed a dependency on LLP1, since it was not functional in *llp1-1* mutants. LLP1 has been reported to act downstream of monoterpene perception in SAR signaling (Wenig et al., 2019). It is known that plants emit volatile cues to establish a SAR response systemically and to confer the SAR response to neighbouring plants. An involvement of LLP1 in *Bt* IR might hint to an airborne mode of signal transmission in IR establishment. Those airborne cues might be emitted by the plant itself similar to VOC communication in SAR. Alternatively, the VOC triggering the LLP1-dependent signal transduction might be emitted by *Bt*. Indeed, *Bacillus* spp. have been reported to emit VOCs which are sufficient to trigger PGPR IR in Arabidopsis (C. M. Ryu et al., 2004). Additional work is required to identify the airborne cues triggering the *Bt* IR and especially, identifying the source of those VOCs, be it bacterial or plant derived.

In contrast to the “canonical” WCS417 IR, *Bt* IR was not dependent on functional JA signaling. This can be concluded from *jar1* plants manifesting a functional IR response similar to that in wild-type Arabidopsis plants. However, *Bt* treatment did lead to a near-significant increase in transcript accumulation of the JA marker gene *VSP1* after pathogenic challenge. Thus, JA might play an auxiliary role in *Bt* IR induction, but is not a prerequisite for full IR manifestation.

Overall, I was able to shed light on plant signaling components involved in *Bt* IR signal transduction. *Bt* IR depends on functional SA biosynthesis as well as on NPR1 and the SAR signaling intermediate LLP1. RT-qPCR experiments revealed priming of genes associated with SA signaling and SAR. Together, the data support a pivotal role of the phytohormone SA and related immune signaling in *Bt* IR in Arabidopsis.

5.2.2 Signal transduction in WCS417 IR

To infer about phytohormones and signaling cues involved in WCS417 IR, I proceeded in a similar manner as with *Bt* IR, and utilized RT-qPCR before and at different timepoints after pathogenic challenges to analyse gene expression

changes associated with IR as well as loss-of-function mutants for functional characterization of WCS417 IR.

WCS417 IR has been shown to be dependent on JA signaling (C. M. J. Pieterse et al., 1998; Pozo et al., 2008; S. van Wees et al., 1999). I could confirm a priming of JA-dependent *VSP1* after root-dip treatment with a WCS417 bacterial inoculant and subsequent pathogenic challenge. However, JA priming seems moderate in comparison to that of SA- and SAR-associated genes, including *PR1, AZI1, EARLI1, FMO1* and *UGT76B1.* This might be due to differences in the sampling time points between this and other studies. Van Wees *et al.*, for example, sampled 1 d, 3 d, 5 d, and 21 d past pathogenic infection, whereas in this study, the samples for RT-qPCR reached a peak 2h-6h after *Pst* induced pathogenic challenge(S. van Wees et al., 1999).

I could further show that WCS417 IR was dependent on functioning SA biosynthesis since the *sid2-1* plants did not show a heightened resistance towards *Pst* after IR treatment. In add-ition, WCS417-treated Col-0 wt plants displayed priming of the SA marker gene *PR1*. Those findings are in contrast to earlier studies by Pieterse and colleagues, who found that WCS417 IR was independent of SA signaling in Arabidopsis (C M Pieterse et al., 1996). Their conclusions were based on experiments with *NahG* transgenic plants. Those plants are in the Col-0 background and contain the bacteria-derived *NahG* gene, which codes for an enzyme degrading SA to catechol. *NahG* plants display a significant and robust reduction of cellular SA levels (Heck, Grau, Buchala, Métraux, & Nawrath, 2003). After WCS417 IR treatment, *NahG* transgenic plants showed a significant drop in the fraction of the leaves with disease symptoms after *Pst* infection in comparison to control-treated *NahG* plants. This is a similar pattern as in Col-0 wt plants and thus led in part to the conclusion that WCS417 IR was independent of SA (C M Pieterse et al., 1996). However, the absolute percentage of leaves with symptoms was higher in control- as well as WCS417-treated *NahG* than in Col-0 wt plants (Figure 26A). If WCS417 IR was completely independent of SA signaling, one might suggest that the disease severity should be the same in Col-0 wt and in *NahG* plants following WCS417 treatment. Pieterse *et al.* also monitored the proliferation of *Pst* in the leaves 5 dpi in Col-0 wt as well as *NahG* plants following control, WCS417 IR, SA or INA treatment. INA is an SA mimic, which is not metabolized by NahG. In wt plants, only control-treated plants showed a significant

proliferation of *Pst* in the leaves. In *NahG* plants, control- and SA-treated plants showed an even higher amount of *Pst* cfu/g of leaves than in wt plants. WCS417-treated *NahG* plants also showed an increase in foliar *Pst* titres, albeit to a lower degree than control- and SA treated plants. INA treatment in *NahG* plants was the only treatment without *Pst* proliferation (Figure 26 B). Thus, there seems to exist at least a partial disruption of WCS417-IR in *NahG* plants against *Pst*. Later comparative studies with the SA biosynthesis defective mutant *sid2* showed that *NahG* plants mounted additional characteristics in plant signaling that were independent of SA availability. These include reduced camalexin production, reduced ethylene emission and delayed JA signaling (Heck et al., 2003). Additional experiments further showed that the product of SA catabolism by NahG, namely catechol, interferes with several processes in plant-microbe interactions. It can lead to loss of non-host resistance in Arabidopsis, change colonization patterns and biofilm-formation in beneficial bacteria and increase ROS, especially H_2O_2 (S. C. van Wees & Glazebrook, 2003) (Thimmaraju Rudrappa, Quinn, Stanley-Wall, & Bais, 2007). Heightened H_2O_2 levels due to *NahG* transgenes have led to lesions in a light- and age-dependent manner in rice (Y. Yang, Qi, & Mei, 2004). On the other hand, H_2O_2 has been reported to be an important antimicrobial agent as well as signaling component in plant defence (Low & Merida, 1996). Thus, the question arises, if *NahG* transgenic Arabidopsis plants are the right tool to prove an SA-independent signaling mechanism of WCS417 IR in Arabidopsis. Additional experiments with *sid2NahG* double mutants in the same setting would be an appropriate way to retest this hypothesis.

The second argument towards SA-independent signaling in WCS417 IR in the work by Pieterse *et al*. (1996) was of the fact that transcript accumulation of the SA marker gene *PR1* was not induced by WCS417 prior to a challenge inoculation of the plants with *Pst*. A monitoring of transcript accumulation after pathogenic infection has not been reported in this study (C M Pieterse et al., 1996). This result does concur completely with my experimental data: I could detect no induction of PR1 transcript accumulation by WCS417 treatment alone, either. Rather, the transcript accumulation of *PR1* following *Pst* infection was higher in WCS417 IR than in control treated plants.

The SA-receptor NPR1 is a key hub in phytohormonal crosstalk to react to differing biotic and abiotic stresses in an adequate response. It has been implicated to be of importance in PGPR/F IR signaling in several studies and my results concur with this observation: *npr1-1* loss of function mutants were not able to establish a state of

heightened immunity in comparison to control-treatments (Nie et al., 2017; C. M. J. Pieterse et al., 1998; Stein, Molitor, Kogel, & Waller, 2008). The mode of action of NPR1 in PGPR IR is not fully understood as of yet. Earlier studies suggested a role of NPR1 in the cytosol in contrast to SA-dependent signaling, where it translocates into the nucleus (Spoel et al., 2003). Since I could observe a dependency of WCS417 local IR, NPR1 might play a role in its capacity as a SA receptor in this form of IR.

Jin1 mutant plants deficient in MYC2 transcription did show a reduced infection severity in control-treated plants as well as WCS417 treated plants. WCS417 IR did not reduce

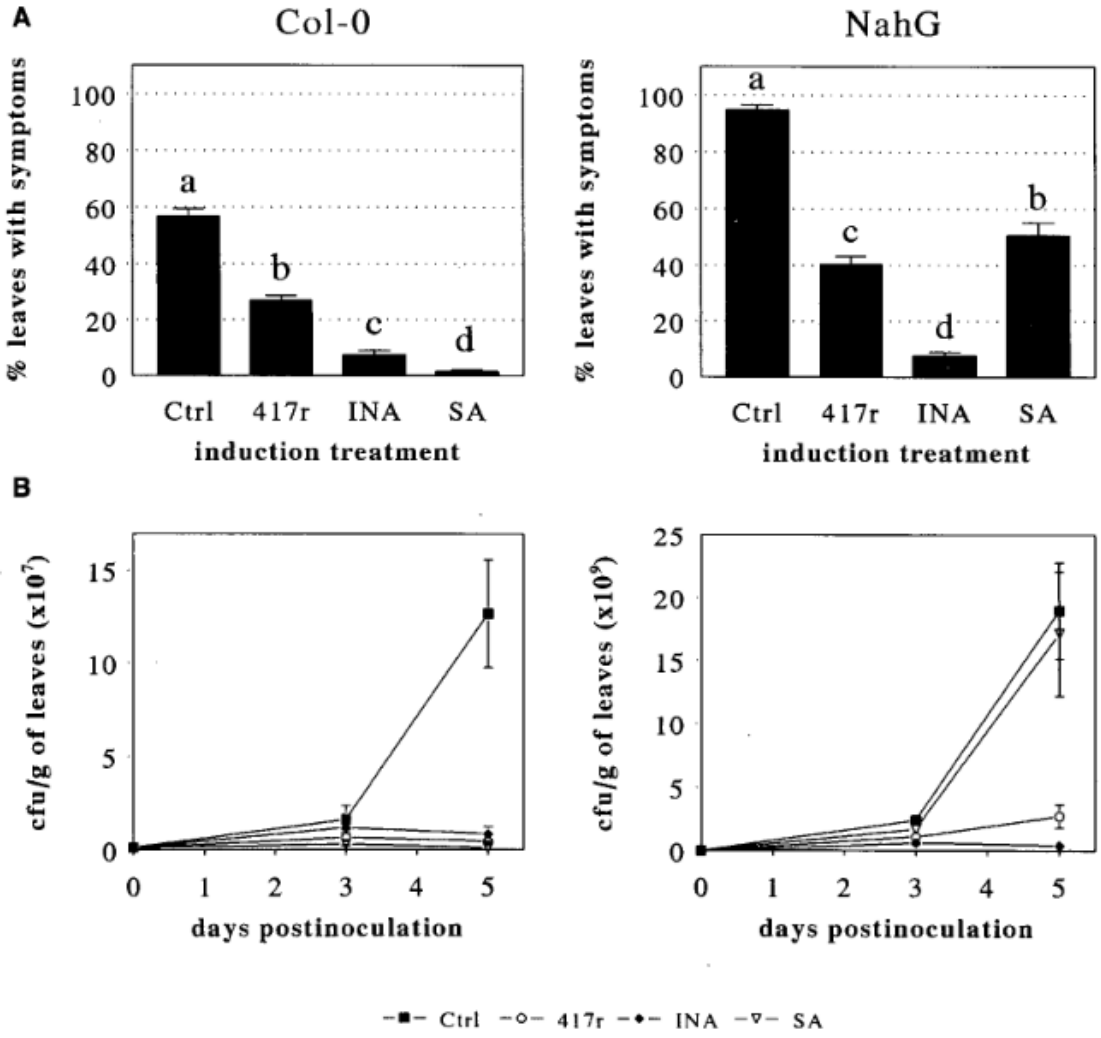


Figure 26: Disease severity and number of pathogens on leaves in Col-0 and NahG plants.

Plants were either control-treated or treated with WCS417, INA (a chemical inducer of SAR) or SAR was induced. A) percentage of leaves with disease symptoms, bars represent mean of 20-25 replicate plants ± SD, characters indicate significant differences ($p<0.05$). B) cfu of pathogens per gram leaf material, points represent mean value of 20 randomly selected leaves ±SD. Adapted from Pieterse et al. 1996

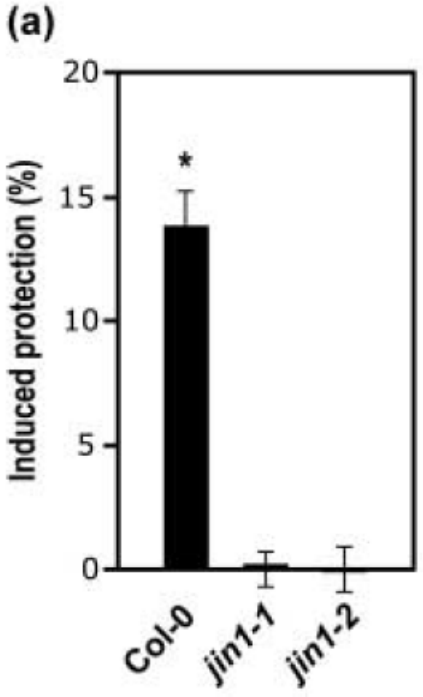


Figure 27: WCS417 IR in Arabidopsis wildtype and MYC2 impaired mutants.

*Plants were treated with WCS417 by being grown in soil containing WCS417 for three weeks. Five-week-old plants were infected with Pst and four days later the disease severity assessed by determining the percentage of leaves showing disease symptoms and was compared to control-treated, naïve plants. * , p<0.05, n= 20 plants. Adapted from Pozo et al. 2008*

the *Pst* titre additionally, though. This is consistent with findings of Pozo et al, who found a heightened immunity in *jin1-2* plants, but no additional enhancement of immunity upon WCS417 treatment (Figure 27). They additionally found that JA-responsive, PGPR IR primed genes showed an enrichment of CACATG motif in the promotor regions (Pozo et al., 2008). This motif is known to be a binding site for MYC2 TF (Abe et al., 1997). They also found a constitutive expression of MYC2 during WCS417 IR. All those findings led them to the conclusion of WCS417 IR being dependent of MYC2. However, in recent years, more knowledge about MYC2 has been accumulated offering new perspectives onto the role of MYC2 in PGPR IR. Nomoto and colleagues found a role of NPR1 in downregulation of MYC2 in an SA-dependent manner (Nomoto et al., 2021). In the absence of JA, MYC2-dependent gene expression is blocked by JAZ proteins binding to MYC2 and thus inhibiting recruitment of TFs and polymerases to the promotor site, as has been described in the introduction of this thesis. Upon increase of cellular JA levels, the JAZ proteins get denatured, and MYC2-dependent gene expression can be induced. If additionally, a rise of cellular levels of SA takes place, NPR1 loses its cytosolic polymer-conformation and translocates into the nucleus, where it can bind to MYC2. While binding to MYC2, NPR1 prohibits recruitment of MED25 and thus restrains MYC2-dependent gene

expression. Thus, NPR1 compensates for the degradation of JAZ proteins in cells with raised JA and SA levels (Nomoto et al., 2021).

In light of these new results, the dependency of WCS417 IR on SA fits to an emerging idea of how WCS417 IR signal integration might work: Upon colonization of roots with WCS417, a so far unknown long-distance signal leads to a heightened perception and/or synthesis of JA in systemic tissues. This leads to MYC2 activation by releasing the repression conferred by JAZ proteins (Pauwels et al., 2010). This MYC2 derepression again leads to repression of the ET-dependent pathway necessary for activation of IR responses towards pathogenic attack (H. Liu & Timko, 2021). If PTI- or ETI-triggered SA signaling is induced by a pathogenic encounter, SA levels will rise intracellularly (C. Vlot et al., 2009). This would lead to relocalisation of NPR1 into the nucleus, where it would bind to MYC2, thus repressing MYC2-dependent signaling (Nomoto et al., 2021; Spoel et al., 2003). In addition, it would inhibit the MYC2-dependent repression of the ET-dependent ERF branch of JA signaling (Figure 28). And thus, JA- and ET-dependent signaling necessary for enhanced resistance against (hemi-)biotrophic pathogens like *Pst*. could be activated (Nguyen et al., 2022; C.-M. Ryu, Hu, Reddy, & Kloepper, 2003; Weller et al., 2012).

This would also explain the heightened resistance in *jin* mutants: without functioning MYC2, the ERF branch will not be repressed, and this might be sufficient for a heightened immunity. In this situation, induction of IR might not be able to grant additional immunity.

In addition to an involvement of JA and SA in WCS417 IR signaling, I could demonstrate a role of pipecolic acid signaling elements in WCS417 IR. On the one hand, there was a priming of *FMO1* transcript accumulation. FMO1 catalyses the final step from Pip to the biological active form NHP and thus sets the Pip signaling cascade in motion. In addition, I found that the *ald1* mutant, which is deficient in Pip biosynthesis, is unable to manifest an WCS417 IR response. SA and Pip are expressed at heightened rate by a self-reinforcing positive feedback-loop in systemic tissue following SAR and a subsequent pathogenic challenge in an NPR1-dependent manner (see 1.7.2 Phytohormones involved in plant immunity). The priming of *UGT76B1*, which I found upon WCS417 IR might fit well into this picture. UGT76B1 is an UDP-glycosyltransferase, which can glycosylate SA, NHP and isoleucic acid to render them biologically inactive (Bauer et al., 2020; E. C. Holmes, Chen, Mudgett, &

Sattely, 2021; Mohnike et al., 2021; von Saint Paul et al., 2011). *UGT76B1* gene expression is upregulated during SAR upon pathogenic challenge most likely to avoid overaccumulation of SAR-inducing agents (von Saint Paul et al., 2011). This is important in order to control cellular SA and NHP levels to finetune and balance the plant's reaction to pathogenic stress in relation to possible other stressors which might arise. A similar mechanism might be triggered after pathogenic encounter in WCS417 IR. To my knowledge, to this point, the role of Pip in PGPR IR has not been investigated. And indeed, the search terms "ISR Pip plant" (or "PGPR IR Pip plant")

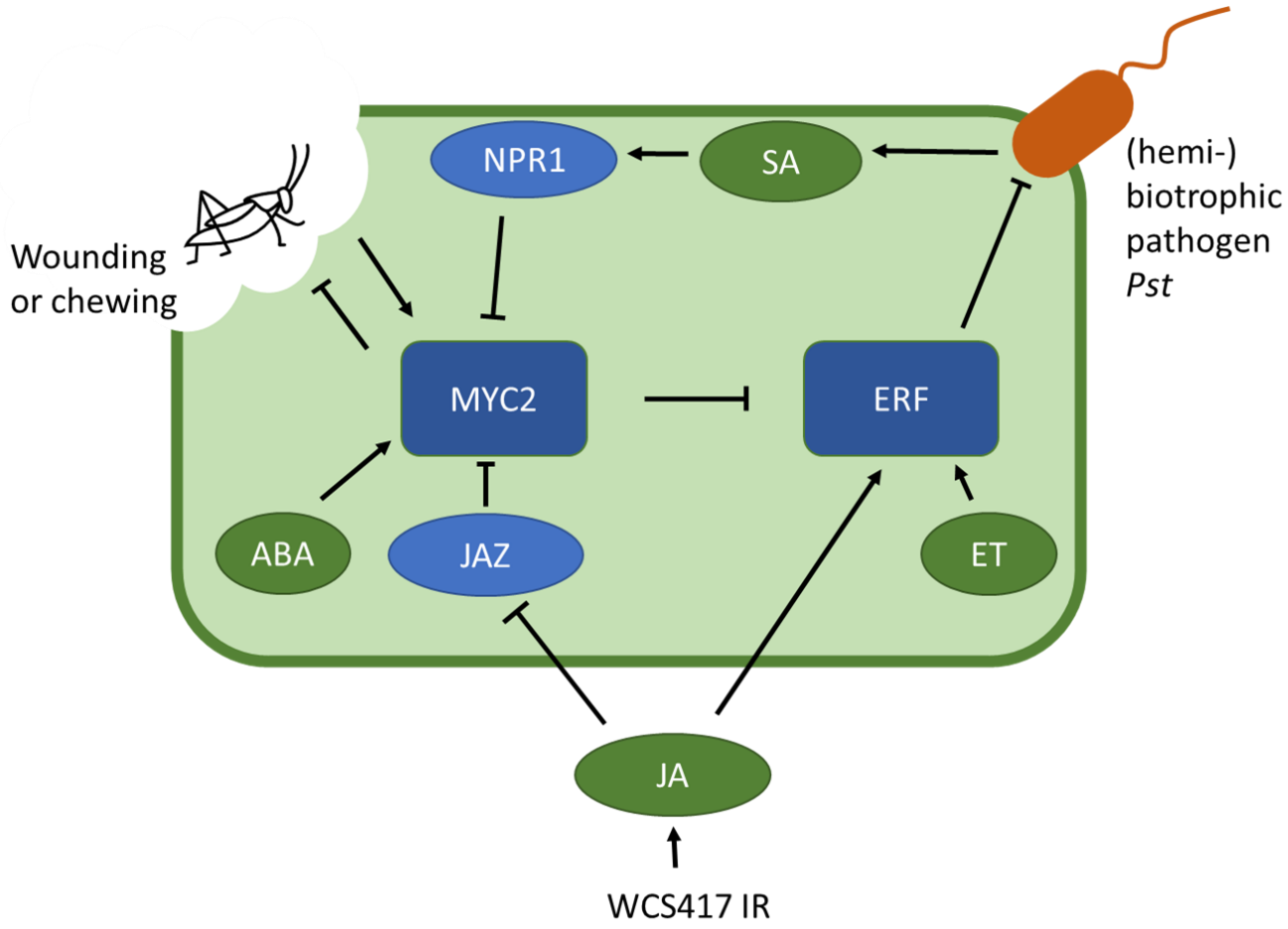


Figure 28: Proposed mode of action of SA and NPR1 in IR mediated resistance against Pst:

WCS417 triggers JA dependent signaling, which can activate two distinct signaling pathways: The ABA-dependent MYC2 pathway, which is blocked by JAZ proteins in the absence of JA. The MYC2 pathway itself blocks SA synthesis as well as the ethylene dependent ERF branch of JA signaling. Upon perception of (hemi-)biotrophic pathogens, SA synthesis is increased, which leads to an NPR1 dependent repression of MYC2 signaling and thus to an activation of the ERF-branch of JA signaling, which is known to be involved in resistance to pathogens.

did not retrieve any results on pubmed (NCBI Resource Coordinators). It is conceivable, that Pip signaling in local WCS417 IR is induced in a self-fortifying feedback-loop after induction of SA signaling in a similar manner as in SAR-signaling. This would lead to the upregulation of *UGT76B1* as I have been able to observe in my experiments.

In addition, I could demonstrate priming of *AZI1* and its close paralog *EARLI1* in WCS417 IR in Arabidopsis. This is again in congruence with previous reports: Cecchini et al. (2015) reported that AZI1 and EARLI1 are prerequisites for successful establishment of WCS417 IR in Arabidopsis (Cecchini et al., 2015). *AZI1* and *EARLI1* play important roles in the transport of the defence-associated, long-distance signal azelaic acid (AzA), while transcript accumulation of both genes is increased upon AzA signaling (Cecchini et al., 2015; Jung et al., 2009). AzA hast been reported to prime SAR-like responses *PR1* transcript accumulation if applied to the leaves (Jung et al., 2009). Additionally, AzA is on the one hand involved in SAR signaling downstream of PiP (C. Wang et al., 2018). On the other hand, transcript accumulation of AZI1/EARLI1 is induced downstream of monoterpene perception in systemic tissues (Riedlmeier et al., 2017). When applied to the roots, AzA primes PGPR/F IR-like responses independent of *PR1* (Cecchini et al., 2019). The exact mechanisms of priming oftentimes remain elusive as of yet. Recently, the chromatin factor MOM1 has been implicated in the repression of priming against pathogens by regulation of histone function. Pip and AzA application inhibited MOM1 function and thus led to an increase of transcripts of MOM1-associated immune receptors, including NLRs and PRRs. These MOM1-NLR/PRRs include for example RECEPTOR-LIKE KINASE7 (*RLK7*) and ACTIVATED DISEASE RESISTANCE 1 (*ADR1*) which are associated with the detection of plant-pathogen interactions (Miranda de la Torre et al., 2023). Since WCS417 is not able to synthesize and export AzA, the main question is, which role priming of *AZI1/EARLI1* plays in the elucidation of IR. Is it dependent on Pip signaling in WCS417 IR, perhaps after perception of VOCs? Or is it active in a Pip-independent, not yet understood role of long-distance signaling? I would suggest further experiments on that topic to shed light on that question.

Another group of long-distance signals employed by plants as well as microbes to confer defence information are the airborne cues of volatile organic compounds. WCS417 has been reported to induce IR at least in part by emitting VOCs, which are sufficient for a full manifestation of IR in Arabidopsis (Desrut et al., 2020; C. Zamioudis

et al., 2015). In SAR, Arabidopsis plants are known to emit monoterpenes, including α- and β-pinene, to relay the systemic signal intra- and inter-*planta* (Riedlmeier et al., 2017). The *ggpps12* mutant, which is unable to synthesize the precursor of those monoterpenes was unable to mount a SAR (Wenig et al., 2019). Thus, not only VOCs emitted by the microbes, but also VOCs emitted by the plant itself seem to play a role in signal propagation of PGPR/F IR. Since AZI1 and Pip have been implicated in SAR resistance signaling downstream of monoterpene perception, this raises the question whether there might be a similar mechanism at play in WCS417 IR, since it seems to be dependent on the same signaling components.

Since the IR triggering microbes, i.e. WCS417 did not only dwell in the roots, but also reached and proliferated in the phyllosphere, I also tested the induction of defence reactions through leaf-associated WCS417. Infiltration of WCS417 into the leaves alone did not trigger any kind of systemic defence. However, a subsequent infiltration of *Pst* two days after WCS417 infiltration into the same leaves led to reduced *Pst* titres. Since this reduction of *Pst* titres was dependent on functional NPR1, it seems prudent to exclude a mere microbe-microbe interaction as the reason of reduced *Pst* titres. This argument is backed by the lack of antagonism in the plate-basted interaction assay. The presence of WCS417 in the leaves might still be contributing to the systemic resistance initiated at the roots of Arabidopsis. Paasch *et al.* for example describe a kind of maturation of PTI after prolonged exposure to PTI-inducing MAMPs. They connect this to age-dependent immunity. In their study, a dysbiotic SynCom associated with plant disease symptoms overstimulated the plant immune system, whereas an eubiotic SynCom was necessary to develop an appropriate immunocompetency (Paasch et al., 2023). Similar to their findings, WCS417 in the leaves might activate PTI in the leaves through long-term exposure and by this complement systemic immunity induced at the roots (Nakano & Shimasaki, 2024).

So, in conclusion, I was able to demonstrate that *Bt* is capable of eliciting a systemic IR response at the roots of Arabidopsis in an SA dependent manner. WCS417 on the other hand triggered an IR response by colonizing roots as well as leaves after root-dip treatment. This IR response elicited IR via JA as well as SA and Pip dependent pathways. So, WCS417-triggered IR neither conforms to the traditional definition of ISR, which refers to systemic IR in response to a root interaction with beneficial microbes (Pieterse *et al.*, 2014), nor to that of SAR, which refers to systemic IR in response to a leaf interaction with a pathogen (Vlot *et al.*, 2021). Thus, this data

supports suggestions made by De Kesel and colleagues (Kesel *et al.*, 2021) that the distinction between ISR and SAR is blurring and that a new terminology such as local versus systemic IR might be more appropriate to conceptualize IR across different plant-microbe interaction systems.

5.3 MICROBIAL CHANGES IN THE PHYLLOSPHERE UPON PGPR IR ELICITATION

Until now, I followed the journey of PGPR-induced resistance from the roots throughout the plant, arriving now at the biggest microbial habitat we have on this planet: researchers estimate the leaf area on earth to be around 508,630,100 km^2, with a bacterial cell density of 10^6-10^7 bacteria/cm^2. This makes the phyllosphere a unique habitat for approximately 10^{26} of bacterial cells (Julia A. Vorholt, 2012). Those bacteria fulfil important functions for the plant and the environment and could be utilized to help cope with arising challenges, including air pollution (Gao et al., 2024; Wei et al., 2017). To achieve this, a better understanding of the composition and function of the phyllosphere microbiome as well as its dynamics in interaction with the plant is necessary.

5.3.1 Microbial changes in Bt IR

In the previous chapter, I confirmed that most of the regulatory changes happening in the plant upon the induction of PGPR IR depend on priming. This is a very important mechanism in the defence-growth trade-off, allowing plants to prioritize growth over defence up to the point of a pathogenic encounter. This kind of balance of resource allocation between growth and defence is an important mechanism, especially for agricultural applications of PGPR as substitution or supplement to classical pesticides: A direct activation and upregulation of defence responses independent of the presence of pathogens would lead to diminished growth and yield due to disadvantageous resource usage.

I aimed to explore the influence of priming in PGPR IR on the microbiome phyllosphere of the plant: Is there still an impact on the microbial composition of the leaves, despite

the changes in transcript accumulation in the leaves being rather moderate. This in in contrast to previous studies of phyllosphere microbiome with more drastic changes of the plant immunity, for example, by utilizing plans with complete knockout of immunity-related genes (T. Chen et al., 2020; Pfeilmeier et al., 2021). Since those previous studies have shown the importance of the phyllosphere microbiome on plant health, I wanted to infer on the changes of the phyllosphere microbiome upon PGPR IR. The least changes could be found in the *Bt* IR treated plants. The overall composition did not change in a significant manner between the IR and control treatments. However, we found one bacterial strain enriched in the phyllosphere after *Bt* treatment in a near-significant manner. This strain, *Solimonas terrae*, has been first described in 2007 and is a Gram-stain-negative, motile and aerobic bacterium with a rod shape (M. K. Kim et al., 2007; S.-J. Kim et al., 2014). It possesses a single flagellum, grows in a temperature range of 15-33°C and has a surprisingly narrow spectrum of assimilated organic substrates. *S. terrae*, for example, tested negative for assimilation of D-glucose, L-arabinose, D-mannitol, N-acetlyglucosamine, maltose, capric acid, adipic acid, and malic acid. Thus, this bacterial strain seems to be adapted to a specific ecological niche. *Solimonas* spp. have been reported to be enriched in the rhizosphere following cold-plasma treatment in sunflower as well as Arabidopsis. In this context, *Solimonas* spp. has been shown to be growth- and defence enhancing (I. Tamošiūnė et al., 2020; Inga Tamošiūnė et al., 2020). *Solimonas soli* has been reported to possess a monooxygenase which is capable of oxidizing small volatile alkenes (to which signaling VOCs like ethylene, pinene, β-nonanal and others belong (Brambilla et al., 2022; Wenig et al., 2019))(Binder, 2020; Riedlmeier et al., 2017), however, it is not capable of growing with those as a sole carbon source (S. N. N. Yang, Haritos, Kertesz, & Coleman, 2024). It thus seems prudent to pursue further experiments with *Solimonas* spp. in the context of plant defence to infer on its ecological niche and properties towards plant health.

Overall, despite the slight (but not significant) enrichment of this very promising bacterial strain, microbial changes in the phyllosphere following *Bt* IR seem to be moderate to non-existent. Those comparatively moderate phyllosphere microbiome changes in response to *Bt* IR likely reflect the fact that *Bt* IR is established as a form of priming by root colonization (U. Conrath, G. J. Beckers, C. J. Langenbach, & M. R. Jaskiewicz, 2015; Mauch-Mani et al., 2017). During priming, the bulk of defence-associated molecular responses do not become evident before a pathogen challenge

(Martinez-Medina et al., 2016). Therefore, it is not unexpected that the microbiome also displays only a moderate to minute responses to the induction of *Bt* IR

5.3.2 Microbial changes in WCS417 IR

The microbial changes in the phyllosphere of WCS417 IR-treated Arabidopsis plants were much more pronounced than those of *Bt* IR treated plants. There was a significant difference in the α- as well as β-diversity between the leaf microbiome of control and IR-treated plants with a significantly lower α-diversity in IR-treated plants. The reason for this is to be found in the significant enrichment of WCS417 itself as well as a significant enrichment of a *Flavobacterium* spp. (ASV4). On average, both make up well over 10% of all reads each in WCS417 IR-treated samples. The capacity of WCS417 to reach the phyllosphere is at odds with former reports, though the reason might be found in the different experimental set ups. Whereas Pieterse *et al.* planted sterile grown seedlings into soil, which has been drenched with WCS417, I treated the roots of seedlings with a liquid bacterial suspension (C M Pieterse et al., 1996). In additional experiments with iodine-stained water, I could show that water is likely rising along the surface of the hypocotyl and thus might be transporting WCS417 along with it (Figure 8). The driving force behind the water movement might be capillary and adhesive effects. This is a possible reason why WCS417 reaches and consecutively proliferates in the phyllosphere after root-dip treatment in contrast to soil-drench treatments. The cause for the pronounced changes in phyllosphere microbiome composition after WCS417 IR treatment in comparison to *Bt* IR treatment might be found directly in the presence of WCS417 itself in the phyllosphere. This presence might lead to microbe-microbe interaction interactions inducing shifts in bacterial abundance. On the other hand, the prolonged activation of PTI responses in the leaves and the following enhanced local induced resistance might lead to differing microbial communities by microbe-plant-microbe interactions.

To infer further on the growth dynamics of the other bacterial strain enriched in the phyllosphere, I utilized Leaf82 from the At-LSPHERE collection (Bai et al., 2015). Leaf82 16S rRNA sequence shares 100% sequence identity to ASV4 found in the Arabidopsis phyllosphere. In plate-based interaction assays, growth capacities of neither Leaf82 nor WCS417 were influenced by each other (Figure 10). Thus,

proliferation of Leaf82 might rather be based on plant-microbe interactions instead of direct microbe-microbe interactions. And indeed, in additional assays of bacterial growth on Arabidopsis plants, WCS417 did not increase Leaf82 titres in wild-type plants in comparison to Leaf82 inoculation alone. On the contrary, in *npr1-1* Arabidopsis plants, the growth of Leaf82 was reduced after prior inoculation of WCS417. NPR1 is essential in both systemic induced resistance, SAR and PGPR IR as well as basal resistance (Ding et al., 2020). If the proliferation of Leaf82 in the presence of WCS417 depends on functional plant immune signaling, this is a strong indicator for plant interference in Leaf82 growth together with WCS417.

Leaf82 belongs to the species *Flavobacterium johnsoniae,* which has been described to have biocontrol properties (Sang & Kim, 2012). *F. johnsoniae* has been reported to emit volatiles directly inhibiting growth of *Phytophtora* in the rhizosphere of pepper (Sang & Kim, 2012). Other members of the family Flavobacteriaceae have been implicated in rhizosphere-mediated pathogen control, either by direct microbe-microbe interaction, or by priming plant defence responses (M. Kolton, Frenkel, Elad, & Cytryn, 2014; M.-J. Kwak et al., 2018; Xue et al., 2015). Following this information, it was important to test whether the reduced *Pst* titres in response to WCS417 IR were due to a direct interaction between *Pst* and Leaf82 or rather based on activation of plant immune responses. The presence of Leaf82 in the phyllosphere of WCS417 IR-treated plants was not responsible for reduced *Pst* titres through a direct microbe-microbe interaction: in a plate interaction assay, I could not detect direct antagonism between Leaf82 and *Pst*. Also, inoculation of *Pst* into leaves which had been inoculated with Leaf82 2 d before, did not lead to reduced propagation of *Pst*, neither in Col-0 wt nor in *npr1-1* plants. From this, I can conclude that Leaf82 does not directly inhibit *Pst* growth by competition for nutrients or through release of antimicrobial components. On the other hand, Leaf 82 was able to elicit a SAR response, effective against *Pst*, if inoculated into the lower leaves of Col-0 wt plants. This systemic resistance was dependent on functional NPR1 and thus indicative of a microbe-plant-microbe interaction: Leaf82 does trigger an immune response of the plant, which in turn reduces *Pst* proliferation in the leaves. Thus, it seems that a *Flavobacterium* is recruited to the phyllosphere following root-dip treatment of WCS417 with subsequent WCS417 proliferation in the leaves. There, Leaf82 is capable of eliciting SAR from there. One might speculate that this is a novel form of the well-described “cry for help”-mechanism, which usually takes place at the roots: plants are capable of recruiting beneficial

bacteria to the roots either as a response to pathogenic attack or perception of certain beneficial bacteria by releasing organic compounds into the rhizosphere. Those compounds are selective towards beneficial bacteria, which in turn are capable of inducing systemic resistance in the plant (Rolfe, Griffiths, & Ton, 2019; Z. Wang & Song, 2022). It is conceivable that similar processes might be at work in the phyllosphere in the plant to enhance immunity priming.

Besides being known to reside in the phyllosphere of plants, the genus *Flavobacterium* has been reported to have excellent root colonizing capabilities and is enriched in the rhizosphere of several plants in comparison to the surrounding soil (Max Kolton, Erlacher, Berg, & Cytryn, 2016; Kraut-Cohen, Shapiro, Dror, & Cytryn, 2021). Since I focused on the leaf microbiome of the plants, I did not test for an additional recruitment of *F. johnsoniae* to the roots. This might be a good pointer for additional experiments in the future. In addition to the defence enhancing properties, *F. johnsoniae* has been described to pertain growth promoting qualities. Most of the *F. johnsoniae* strains known so far are capable of synthesizing IAA, an auxin which stimulates plant growth (McBride et al., 2009). *F. johnsoniae* is also capable of solubilizing phosphate and thus making it accessible for plants to further enhance plant proliferation (Soltani et al., 2010). And indeed, I could observe increased plant growth after leaf-treatment with Leaf82, confirming the growth-promoting properties for *F. johnsoniae* strain Leaf82.

The mode of action for leaf enrichment is at this moment not entirely clear. Direct recruitment by WCS417 seems not to be a likely means for this enrichment. This is reinforced by the fact that WCS417 is capable of acidifying its surroundings in soil to escape plant PTI responses (Ke Yu, Liu, et al., 2019). *F. johnsoniae* relative abundance has been reported to decline in acidic soils (Max Kolton et al., 2016). If WCS417 employs a similar strategy of acidification in the phyllosphere, that would be antagonistic towards *F. johnsoniae* proliferation. One possible explanation might be the accumulation of callose, and other polymers used to fortify cell walls. *F. johnsoniae* genomes have been reported to be rich in genes coding for polymer-degrading enzymes such as β-glucans, chitinases, and mannosidases among others (McBride et al., 2009). Since WCS417 IR is reported to prime callose deposition and β-glucanases are capable of degrading callose (Van der Ent et al., 2009), there might be a connection to be found between priming of WCS417 IR and *F. johnsoniae* enrichment.

Another possible explanation lies in immediate transcriptomic changes following WCS417 colonization of the roots. I was not able to capture direct gene induction following root dip inoculation but sampled for RT-qPCR 24 d after PGPR IR treatment. In previous reports, however, colonization of Arabidopsis roots or exposure to WCS417 volatiles did lead to some major changes in gene transcript accumulation in aerial tissues at 7 dpi. Especially genes involved in sugar transport were induced upon WCS417 IR induction, leading to increased nutrient relocation and elevated root growth (Desrut et al., 2020). Thus, immediate changes in gene regulation do take place and might also influence microbial composition.

Overall, I was able to explore the passage of PGPR IR signal generation from the region of origin, the roots, to the area where it manifests, i.e. the aerial tissues. I could determine signaling components involved in the signal transmission and could show that WCS417 IR does change the microbiome of the phyllosphere, whereas *Bt* IR does not. Thus, I could show that “traditional” PGPR IR, which is induced at the roots does not exert a major influence on the phyllosphere microbiome The WCS417 induced microbial changes were putatively based on local immunity responses elicited by WCS417 at the leaves of the plants due to long-term PTI responses as well as direct microbe-microbe interactions. The presence of WCS417 in the leaves enables the plant further to respond to upcoming, unfavourable events in an adequate manner: by recruiting additional beneficial microbes which prime further immune responses in a SAR-like fashion. Thus, the plant is able of further heightening its pathogenic resistance without undue resource allocation to defence in the absence of pathogens. I suggest further research on the possible new beneficial microbial *F. johnsoniae* strain Leaf 82 and its growth promotive as well as plant protective properties.

6. OUTLOOK

6.1 IR AND INVOLVED PLANT SIGNALING COMPONENTS

In this work, I was able to show that *Bt* is capable of eliciting IR in Arabidopsis. A next step could be to evaluate a potential role of *Bt* to elicit IR in monocots like barley or rice. The insecticidal and nematicidal properties could help to prevent soilborne pests diminishing yield. So, plants could be protected from plant pathogens and pests at the same time so secure crop harvests. However, great care has to be exerted in the use of viable *Bt* cultures, since *Bt* is closely related to the pathogenic strain *Bacillus cereus* (Ehling-Schulz, Lereclus, & Koehler, 2019). Horizontal gene transfer is a common way to gain new characteristics in bacteria and virulence genes are easily gained this way (X. Hu et al., 2020)[1].

In addition to proving the IR-eliciting properties of *Bt*, this study suggests the involvement of SA in the signaling against (hemi-) biotrophic pathogens in WCS417 IR as well as *Bt* IR. I have proposed a new mode of action of SA in the signal transduction of IR. Specifically, I propose that SA in cooperation with NPR1 blocks MYC2-dependent gene expression and thus hinders the repression of the ERF-pathway by MYC2. This helps to prevent hijacking of the plant immune system by pathogens: *Pst* can introduce coronatine into the plant cell in order to block the JAZ proteins otherwise blocking the MYC2 pathway. Additionally, coronatine boosts the MYC2 pathway by enhancing the ABA concentration in the plant cell. In the past, the main body of research on SA dependence of IR against (hemi-) biotrophic pathogens has been conducted with *Pst*, which is able to produce and inject coronatine via the type-III secretion system (T3SS) (Kojima et al., 2013; Nguyen et al., 2020; Nie et al., 2017; van de Mortel et al., 2012). Thus, it would be of interest to test this hypothesis by infecting *npr1* mutants with a *Pst* strain lacking either the gene for production of coronatine or even the T3SS. The results of such an experiment would provide insight

[1] If one dares to dream really big, synthetic codon compression and codon reusage inspired by synthetic biology would be a sure means to disable functioning horizontal gene transfer. This means completely rewriting the genetic code to use less synonymous codons per amino acid and assigning the now free codons to new amino acids, thus rewriting the universal genetic code into a specific “dialect”. This renders the bacterium unable to handle genetic code acquired via horizontal gene transfer (Atkinson, 2019).

into the interaction of MYC2 and NPR1 in plant immunity towards *Pst.* This might additionally shed light on the role of SA in JA mediated immunity via the JA/ET dependent ERF signaling pathway.

6.2 Phyllosphere microbiome changes upon IR elicitation

At this point, this journey, as well as this thesis, comes to an end. I begun at the roots, followed the systemic resistance throughout the plant, and investigated the microbial communities in the leaves. Thus, I gained insight into how the plant and its microbial inhabitants interact and form something bigger than just the sum of its parts: a holobiont, capable of adjusting to adverse environmental conditions faster and more precisely than the plant alone would ever be able to. I started out with the question, whether the induction of PGPR IR at the roots would change the composition of bacteria in the leaves of the plants. I can now answer with great clarity: It depends…

If on the PGPR IR follows “just” a priming, as I have observed with *Bt* IR, the changes in the phyllosphere microbial community seem to be minute at best. If the PGPR IR is accompanied by further transcriptional changes or interacts with other forms of induced resistances, it might be of more consequence to the phyllosphere microbiome. A putative local IR interaction, perhaps a prolonged PTI interaction with WCS417 at the leaves might have led to the enrichment of a *F. johnsoniae* in the phyllosphere of Arabidopsis. This can be followed by a general heightened immunity and promoted growth induced by this beneficial bacterial strain.

With these results, I contribute to our understanding of plant and microbiome as a regulatory unit. With his understanding, we can overcome many man-made obstacles which we are facing at the moment. Better adapted microbial communities at the roots can improve drought resistance and heat tolerance to help adapt plants to climate change (Alsharif et al., 2020). Suitable microbiomes can help to reduce the need for synthetic fertilizers, thus reducing the energy needed for nitrogen fixation and mining of phosphate rock (Priyadarshini, Choudhury, Tilgam, Bharati, & Sreeshma, 2021). And finally, by introducing suitable bacteria into the phyllosphere microbiome, we could reduce air pollution (Franzetti et al., 2020). This can be achieved by utilizing bacteria capable of fixing atmospheric compounds, which are toxic for humans but can be incorporated into microbial energy metabolism.

However, all this is only achievable in a sustainable manner with a firm grasp of mechanics underlying plant-microbiome interactions and an understanding of how environmental cues influence those dynamics.

If I had to suggest ensuing research questions to follow this quest of deepening our understanding of plant-microbial interactions, I would point first of all towards broadening the focus: I only gained insight into a small fraction of the microbiome: the bacterial part. I completely neglected the impact of IR on fungi, archaea, and protists since it would have gone beyond the limits of this work. However, in future experiments, it would be beneficial to include at least the fungi into the experimental setup. Fungi are the best studied subgroup of the microbiome besides bacteria, so amplicon sequencing via ITS is well-established and the results can be put into the broader context of already existing knowledge.

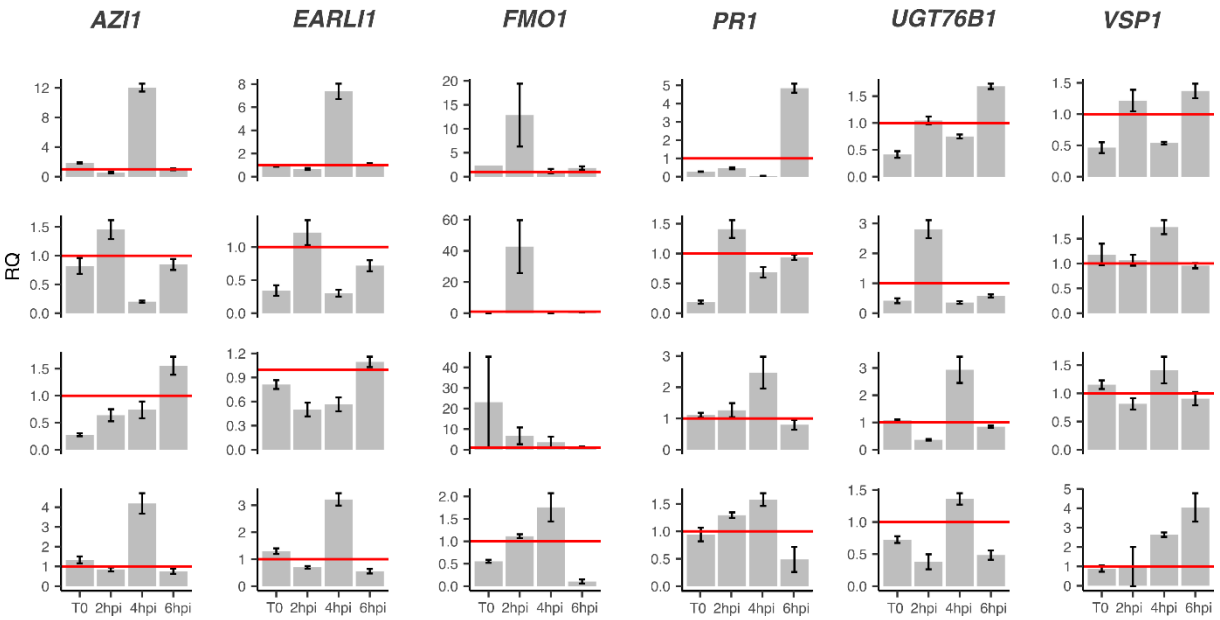
Another interesting question would be, if changes of the microbiome upon IR elicitation could be found in the seed microbiome and thus could conveyed to future generations. Bziuk *et al.* found a connection between microbiome diversity and ability of being primed against pathogens (Bziuk et al., 2021). In addition, Bakker *et al.* proposed the concept of long lasting protection gained by beneficial microbes in the rhizosphere to offspring via the soil-borne legacy (Peter A. H. M. Bakker et al., 2018). So why not hypothesise that this protective characteristic may also be passed on via the seed microbiome.

The next question would be that of the plant protective properties and its mechanism of conveyance in the bacterial strain *Solimonas terrae*. This strain is obtainable from the DSMZ, so further experiments are called for to gain insight into how it interacts with plants. The logical next step would be to infer if *S. terrae* and Leaf 82 also confer a heightened resistance against pathogens in other plants, especially crop plants and if this comes at a cost regarding yield.

There are many more points to continue this research, always towards the goal of understanding plants and microbes better. And as interesting this path may be, it will always be a means to an end, with the final aim always being to help secure food and a healthy environment for mankind to thrive in.

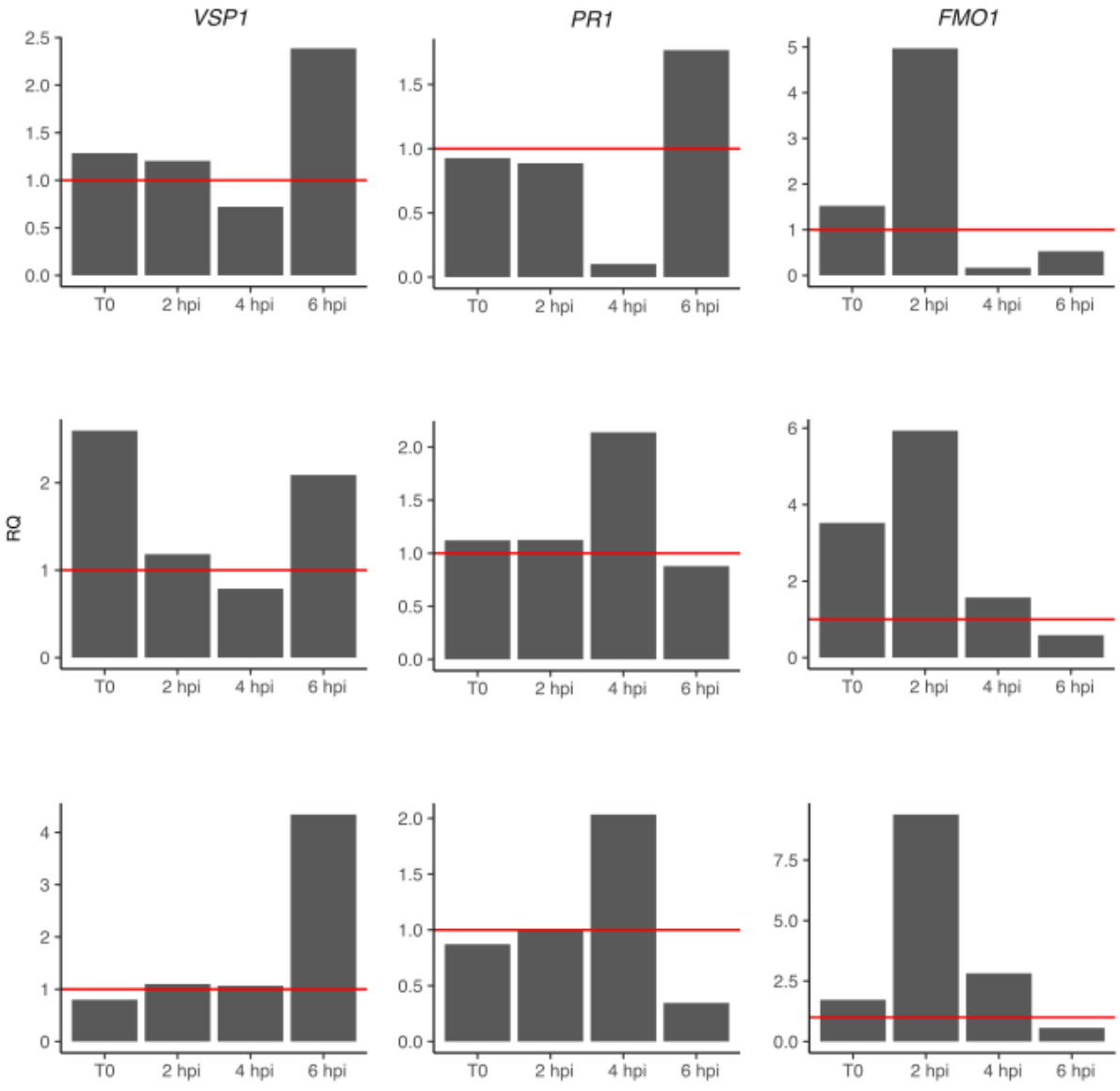
7. SUPPLEMENT

List of supplementary Figures



Supplementary Figure 1: Transcript accumulation of AZI1, EARLI1, FMO1, PR1, UGT76B1, and VSP1 before (T0) and at 2, 4, and 6 hpi as indicated below the panels.

The roots of 10-day-old, sterile-grown Arabidopsis seedlings were inoculated with WCS417 (grey bars) or a corresponding control solution (red horizontal lines). Following 3.5 weeks on soil, the leaves of the treated plants were infiltrated with P. syringae pathovar tomato (Pst). Leaf samples were taken before infection and 2h, 4h and 6h after infection. Transcript accumulation of AZI1, EARLI1, FMO1, PR1, UGT76B1, and VSP1 was determined by RT-qPCR and normalized to that of UBIQUITIN. Bars represent average RQ-values relative to those in control-treated plants of three technical replicates performed on the same RNA sample ± SE. Different plots originate from biologically independent replicate experiments.



Supplementary Figure 2: Transcript accumulation of VSP1, PR1, and FMO1 before (T0) and 2, 4, and 6 hours post-inoculation (hpi).

The roots of 10-day-old, sterile grown Arabidopsis thaliana seedlings were emerged in a Bt suspension or in 10 mM $MgCl_2$ as the control treatment. After one hour, the seedlings were transferred to soil and propagated for 3.5 weeks. Subsequently, leaves of the plants were inoculated with Pst and leaf material harvested at T0 and at 2, 4, and 6 hpi. Transcript accumulation of VSP1, PR1, and FMO1 was analysed using RT-qPCR and normalized to that of UBIQUITIN. Bars represent transcript accumulation of the genes indicated above the panels in Bt-treated plants relative to the respective $MgCl_2$ controls. Each row of panels represents data from one biologically independent replicate experiment, red lines mark RQ=1, which corresponds to the control-group ($MgCl_2$-treatment).

8. ACKNOWLEDGEMENTS

Most importantly, I want to extend my deepest and heartfelt thanks and appreciation towards my supervisor Prof. Dr. Corina Vlot-Schuster. This thesis would not exist without her. She helped me develop as a scientist via long discussions, hard questions, and by setting an example as to how to approach scientific questions in a constructive and integrous way. She not only helped me to grow as a scientist, but also as a person, by constant encouragement and the wisdom to know when to push and when to just let me try on myself. I would not be the person I am today without her: she helped me to find courage and self-esteem in what I do. Corina is a role model for every female scientist by successfully pursuing her career, being a trustworthy superior and a loving mother all in one person. Her way of guiding young scientists and setting them on the right path in the complex world of science is an inspiration for me.

I want to express my deep thanks to Prof. Dr. Jörg Durner, who enabled me to write this dissertation at the Institute of Biochemical Plant Pathology. He contributed greatly to my thesis by incessant advice, encouragement and support during Thesis Committee Meetings and aside of those. I am very grateful for him being my first examiner for thesis defense.

I am indebted to Prof. Dr. Julia Vorholt and her former Post-Doc student Dr. Sebastian Pfeilmeier for invaluable advice, critical questions, and highly appreciated pointers towards the right research questions and how to approach them in a profound manner. They helped me with technical advice as much as with their profound knowledge and experience.

My heartfelt thanks also go to Prof. Dr. Michael Schloter, whose experience and advice on microbial topics was a highly appreciated and precious contribution to this work and helped to broaden my knowledge in this area greatly. His guidance aided in the progress of this project in a considerable manner. I want to give my thanks to Prof. Dr. Schloter for being willing to be the second examiner for my thesis defense.

I also want to thank Dr. Manuel Spannagl for contributing to my Thesis Advisory Committee and beyond. His advice in everything regarding genetics was a great contribution to my overall understanding and the advance of my thesis.

Last but not least, my sincere thanks go to all the colleagues who accompanied me on this journey, be it in Munich or in Bayreuth. I especially want to mention Marion and Claudia, who diligently performed experiment after experiment to confirm theories and findings of my thesis. They were a trusted and highly appreciated source of experience, advice, help, but also of encouragement, comfort when experiments went awry, and companionship in long days at the institute. More thanks go to my fellow PhD students, most of whom are finished by now: Thank you Miriam Lenk, Kornelia Bauer, Jennifer Sales, Alessandro Brambilla, Shahran Nayem and Samaneh Bagheri for shared advice, shared successes and failures and for being unfailing companions on this rocky road to my thesis.

Ganz persönlich möchte ich mich bei meiner Familie und meinen Freunden, ganz besonders bei meinen Großvätern bedanken:

Harald Jöhnk hat mir die Liebe zur Natur in früher Kindheit nähergebracht und die Komplexität der Zusammenhänge in der Natur begreifbar gemacht. Dadurch hat er meine Füße erst auf diesen Pfad der Neugier gesetzt, dem ich jetzt so viele Jahre gefolgt bin. Joachim Sommer hat mir immer das Gefühl gegeben, alles schaffen zu können, was ich mir in den Kopf gesetzt habe. Dieses Urvertrauen zu spüren, selbst wenn ich es selbst gerade nicht glauben mochte, hat mir manches Mal den Mut zum nächsten Schritt gegeben, auch wenn ich diesen Mut in mir selbst gerade nicht finden konnte. Dieses Gefühl, alles zu schaffen, wenn der Schädel nur dick genug ist und zu wissen, dass er mir den Rücken freihält, wenn ich es am dringendsten brauche, war unschätzbar wertvoll auf dem Weg, diese Arbeit abzuschließen.

Ein ganz großes Dankeschön geht natürlich auch an meine ganze Familie für Zuspruch, Verständnis, Aufmunterung und Unterstützung, wann immer ich das gebraucht habe.

Ein besonderes Dankeschön geht an Nikola, der mich auf die eine oder andere Weise entlang dieses Weges begleitet hat und mir dabei immer den Rücken freigehalten hat. Von ganzem Herzen: Danke! Ohne die vielen lieben Freunde wäre diese Reise durch das Tal des Wahnsinns, dass sich Dissertation nennt, nie zu einem positiven Abschluss gekommen: Danke Fii und Eric, dass ihr mir in den entscheidenden Momenten Heimat, Unterstützung und eure unschätzbare Erfahrung als Autoren habt zuteilwerden lassen. Ohne euch wäre es um meine geistige Gesundheit schlecht bestellt gewesen. Fhtagn! Ein ganz großes Dankeschön geht an Chris, der den gelegentlich furchteinflößenden Pfad der Dissertation vor mir beschritten hat und mir so als Vorbild, aber auch als steter Begleiter Mut und Zuspruch gegeben hat. Vielen Dank euch allen, die ihr mir zugehört habt, wenn nichts vorwärts ging, die ihr mir Trost gespendet habt, mich angefeuert habt und treue Begleiter auf meinem Weg der letzten Jahre wart. Vielen Dank auch an Felix, Sonia, Daniel, Tom, Markus und Andi. Ihr seid toll!

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