

The cry for help:  
How plants orchestrate interactions with  
the rhizosphere microbe.

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## Layman summary

Plants don't just grow alone in soil. They have a whole community of tiny organisms living around their roots called the rhizosphere microbiome. These microbes can function as the plant's helpers, providing various forms of support. In this review we explore how plants and the microbes interact. First, plants and microbes communicate. When plants are stressed, due to lack of nutrients or pathogen attack, they release chemical signals through their roots. These signals attract good microbes to the roots and is called "the cry for help". Next, microbes colonize the roots. Upon signal detection microbes move towards the root and attach to the root surface. A process which is realized by specific proteins that can form a bond between microbe and the root surface. Since the plant cannot distinguish between good and bad microbes, it activates its defense system. In response, good microbes have evolved ways to avoid detection by the plant or suppress the defense system. This allows them to stay on the root and help the plant. Finally, the microbes provide the plant with benefits. Microbes make it easier to absorb nutrients from the soil, help the plant grow better and even protect the plant against diseases and insects. Overall, the interaction between plant and good root microbes is crucial for the survival of the plant and its health. By learning more about how these interactions work, we can develop better ways to grow our crops and protect our food supply.

## Abstract

Plants face numerous challenges throughout their lifecycle, from nutrient deficiencies to pathogen attacks. To navigate these challenges, plants developed complex defense mechanisms. One crucial ally in this is the rhizosphere microbiome. This review explores the intricate relationship between plants and their rhizosphere microbes, elucidating the mechanisms by which plants recruit and benefit from the microbial allies following pathogen infection. Plants utilize various signaling compounds upon pathogen attack, effectively crying out for help and with that attract beneficial microbes to their roots. These beneficial microbes are able to respond to these stress induced signals via chemotaxis which allow them to colonize the roots in two different stages, establishing a permanent position at the root surface. Once established, beneficial microbes utilize sophisticated strategies to interact with the plant host. First these strategies are aimed to evade or suppress the plant immune responses. Followed by mechanisms that allows beneficial microbes to provide plants with different beneficial effects, like better nutrient uptake, growth promotion and pathogen control.

## Introduction

Plants, as sessile organisms, face an array of environmental stresses throughout their lifecycle. These challenges span from biotic stresses such as pathogenic infections and herbivore attacks to abiotic factors including prolonged drought periods and nutrient scarcities. In order to thrive amidst such challenges, plants have evolved an intricate array of defense mechanisms and stress responses, shaped through millennia of evolutionary pressure (Bakker et al., 2018; Pieterse et al., 2012, 2014). These mechanisms encompass a diverse repertoire of biochemical, physiological, and molecular strategies aimed at fortifying the plant's resilience against the ever-changing environment.

A pivotal role contributing to such resilience is played by the rhizosphere microbiome – the complex community of microorganisms inhabiting the soil directly surrounding plant roots. Beyond the occupation of space, these microbes actively engage in symbiotic relationships with the plant, exerting profound influences on its growth, development, and stress tolerance. Plants channel a substantial portion of their metabolic resources towards the roots, with roots secreting up to 40% of the photosynthetic products (Bais et al., 2006). This organic influx transforms the rhizosphere into one of the most nutrient-rich niches on earth. Consequently, the rhizosphere harbors an astounding abundance of microbes, surpassing even the surrounding soil due to what is termed the rhizosphere effect (Bakker et al., 2013). This vast microbial community possesses significantly more functional genes than the plant itself, unlocking additional genetic and metabolic possibilities (N. R. Wang & Haney, 2020).

In order to utilize the potential brought by these additional genes plants engage symbiotic relationships with beneficial rhizosphere microbes. According to the “cry for help” hypothesis plants secrete specific chemical signals or cues via their roots, signaling their distressed state in order to attract microbial allies capable of providing assistance, alleviating the plants predicament (Bakker et al., 2018). Multiple studies have shown such “cry for help” mechanisms. For instance, glycerol-3-phosphate and pipercolic acid accumulation upon prolonged drought conditions to increase the abundance of *Actinobacter* (Song & Haney, 2021), volatile organic compounds (VOCs) released upon herbivory to attract carnivorous insects and alter the rhizosphere microbiome composition (Lee Díaz et al., 2024; Zitzelsberger & Buchbauer, 2015) and coumarin secretion upon pathogen infection to select beneficial rhizobacteria, that can aid in pathogen protection (Stringlis, De Jonge, et al., 2019). However, one of the most well-known and best studied examples, and therefore used as guideline in this review, is the “cry for help” via strigolactone secretion. Plants produce and secrete strigolactones upon nutrient deficient conditions in order to recruit arbuscular mycorrhizal fungi (AMF). Which, once the arbuscular mycorrhizal (AM) symbiosis is established provides the plant with phosphorus and nitrogen in exchange for carbon (Ho-Plágaro & García-Garrido, 2022). These examples show that the rhizosphere microbiome not only acts as a passive beneficiary of root exudates but also serves as an active participant in the plant's defense and adaptation strategies. By harnessing the collective metabolic potential of the rhizosphere microbiome, plants can effectively augment their resilience and survival in challenging environments, underscoring the intricate interplay between plant and their microbial partners in shaping ecosystem dynamics.

The mechanisms underlying the strigolactone dependent “cry for help” and successive AM symbiosis are well understood. This review aims to use these established mechanisms as a guideline to compare with mechanisms involved in the pathogen induced “cry for help”. Specifically, we will delve into the beneficial effects of microbes followed by the cry for help, root colonization and immune suppression. Our goal is to demonstrate how a pathogen-induced “cry for help” can result in beneficial outcomes, while also highlighting the mechanisms that remain elusive.

## Beneficial effects

Beneficial microbes can provide various advantages to plants. In the case of AM symbiosis the extensive hyphal networks serve as extensions of the plant roots system, aiding the plant in the uptake of essential nutrients like phosphorus and nitrogen, while simultaneously facilitating better water absorption (Ho-Plágaro & García-Garrido, 2022). Furthermore, the AM symbiosis contributes to plant protection against pathogens by priming of the immune system, a mechanism called mycorrhiza induced resistance (MIR) (Dey & Ghosh, 2022). Apart from AMF, other beneficial microbes exhibit similar advantageous effects, which can be broadly categorized into three main groups; enhancement of nutrient uptake, plant growth promotion and pathogen control.

### Enhanced nutrient uptake

Iron is one of the most abundant elements on earth, however, it is foremost present in the ferric form ( $\text{Fe}^{3+}$ ) which cannot be taken up by plants. Many microbes produce siderophores, compounds that can effectively chelate unavailable iron, facilitating iron uptake. Interestingly, this mechanism can also be used to promote iron uptake in plants in a microbe dependent manner, as has been shown in studies with *Bacillus* in wheat and *Pseudomonas* in apple (Gao et al., 2022; Yue et al., 2022). Similarly, other essential nutrients such as phosphorus and potassium commonly reside in the soil in inorganic forms, posing difficulties for plant uptake (Das et al., 2022). Remarkably, similar microbial dependent mechanisms have been reported for the mobilization of unavailable potassium and phosphorus. For example, potassium uptake was found to increase when maize roots were inoculated with *Aspergillus* (Muthuraja & Muthukumar, 2021), while root inoculation with phosphorus solubilizing bacteria (PSB) caused enhanced phosphorus uptake, mediated by the release of acidic metabolites, like gluconic acid (Anzuay et al., 2015; Das et al., 2022).

### Growth promotion

One major way in which beneficial microbes promote plant growth is via auxin production. The majority of beneficial bacteria can produce auxin, in the form of indole-3-acetic acid (IAA). In plants, IAA changes the balances of auxin, resulting in phenotypical changes like increased root growth (Lugtenberg & Kamilova, 2009; Olanrewaju et al., 2017; Pantoja-Guerra et al., 2023). However, the plant response to IAA is highly dependent on the plant species, auxin levels within the plant and its developmental stage as reviewed by Olanrewaju et al. (2017). In addition to auxin production, other beneficial bacteria have shown to alleviate stress induced ethylene disbalances, via the bacterial 1-aminocyclopropane-1-carboxylate (ACC) deaminase. As a protection mechanism, plants induce ethylene production upon exposure to abiotic stressors. This however, can have negative impacts on plant growth. The bacterial ACC deaminase reduces ethylene levels, thereby restoring normal growth (Naing et al., 2021). Moreover, similar to the production of IAA, beneficial bacteria also show to be capable of producing other phytohormones like cytokinins, gibberellins and abscisic acid (ABA). Increased levels of cytokinin showed to increase shoot biomass and fruit yield (Tsukanova et al., 2017; Zaheer et al., 2022). Gibberellin homeostasis can be affected by bacterial gibberellins or bacterial induced gibberellin synthesis both of which induce an increase in shoot growth, while the impact of root growth can be either positive or negative (Olanrewaju et al., 2017; Tsukanova et al., 2017). Finally, ABA production by beneficial bacteria can cause plant ABA levels to rise a mechanism which has reported to contribute to drought resistance (Tsukanova et al., 2017). Even though, not all of these mechanisms result in direct growth promotion, tipping the scales in tradeoffs involving plant growth and stress responses, eliminates the otherwise occurring halt in growth.

## Pathogen control

Beneficial microbes play a multifaceted role in restricting the growth of pathogens, with competition being one of the utilized mechanisms. Within the rhizosphere, microbes compete with one another for nutrients and ecological niches, providing an opportunity for beneficial microbes to outcompete pathogens for essential nutrients and space, especially when they engage in nutrient exchange with the host plant. Moreover, many beneficial microbes produce antibiotics that can directly inhibit pathogen proliferation. Notable examples include 2,4-diacetylphloroglucinol (DAPG) produced by *Pseudomonas* species and shown to be involved in take all decline in wheat (Bakker et al., 2013; Hamid et al., 2021; B. Wang et al., 2023), hydrogen cyanide (HCN) which showed to be effective against pathogenic fungi, termites and nematodes (Hamid et al., 2021; S. Wang et al., 2021) and pyoluteorin (Plt) which showed to restrict growth of pathogenic oomycetes as extensively reviewed by (Hamid et al., 2021). In addition to these direct mechanisms, beneficial microbes have been found to induce systemic resistance in plants, enhancing their ability to withstand pathogen attacks. One such mechanism involves the induction of the jasmonic acid (JA) mediated defense response ISR. Upon colonization of plant roots by ISR inducing microbes, a signaling cascade primes the expression of JA and ethylene defense related genes. Priming allows the plant to mount a stronger and faster defense response to future pathogen attacks (Pieterse et al., 2014). Similar to ISR, beneficial microbes can trigger a SA mediated defense response known as systemic acquired resistance (SAR). SAR is a defense mechanism activated throughout the plant following an initial localized infection, providing systemic protection against a wide range of biotrophic pathogens (Tsukanova et al., 2017; Zamioudis & Pieterse, 2012). Beneficial microbes have been found to stimulate this immune response via the production of SA or SA related compounds (Sun et al., 2021; S. Wang et al., 2021). The intricate interplay between plant hormones, such as SA, JA ethylene and auxin, results in a complex hormonal crosstalk network regulating plant immune responses. Beneficial microbes can modulate this hormonal network, finetuning plant defense responses thereby promoting overall health and resilience.

It is clear that beneficial microbes can provide diverse advantages to plants. Direct advantages include the enhanced uptake of essential nutrients and pathogen competition. Whereas, indirect advantages include microbial interference with the plant hormonal network, which has shown to result in growth promotion and induction of systemic defense mechanisms. This however, raises the question how are plants able to recruit such microbial allies, how can they establish themselves among the diversity in the rhizosphere and how do plants discriminate between beneficial and pathogenic microbes? The remainder of this review will focus on answering these questions.

## The cry for help

Recognition is the first critical point in the establishment of a functional symbiosis. The host plant and beneficiary must identify one another amidst the immense diversity in the soil. Plants can orchestrate this via the “cry for help”. As mentioned earlier, when plants experience stress they produce signaling compounds which are secreted into the rhizosphere, where they can be detected by microbes. In the AM symbiosis plants signal their nutrient deprived status through the release of strigolactones, a group of plant hormones renowned for their role as signaling molecules in this symbiosis (Ho-Plágaro & García-Garrido, 2022). These strigolactones signal the presence of the plant and simultaneously attract the AMF, for which they function as chemoattractants. Such a signaling process is, however, not exclusively reserved for the recruitment of AMF upon nutrient deficiency. There are numerous examples in which pathogen infection results in changes in the rhizosphere microbe. For example

wheat plants recruit the beneficial bacterium *Stenotrophomonas rhizophila* in the rhizosphere and endosphere after infection with *Fusarium pseudograminearum* (H. Liu et al., 2021), or tobacco infection with *Ralstonia solanacearum* which recruited beneficial microbes protecting against this bacterial pathogen (Tao et al., 2024). Even though, such changes are often assigned to changes in root exudation patterns, only a limited number of cases identified the actual signaling compound involved in the pathogen induced “cry for help”. These signaling compounds can be divided into soluble root exudates and VOCs.

### Soluble root exudates

Coumarins are secondary metabolites present in the majority of plants and are produced via the phenylpropanoid pathway. Usually coumarins are produced and secreted into the rhizosphere during iron deficient conditions. Once in the soil coumarins can aid in the chelation and mobilization of unavailable iron as part of an iron uptake strategy (Stringlis, De Jonge, et al., 2019). Beside their role in iron chelation, coumarins can also be used as plant signaling compounds. Upon pathogen infection, many different plant species have reported to orchestrate the secretion of these secondary metabolites (Stringlis, De Jonge, et al., 2019). Once released coumarins exhibit selective antimicrobial properties which allow them to repel certain microbes, including but not limited to the pathogens, *Alternaria alternata*, *Botrytis cinerae*, *Pseudomonas syringae* and *Tobacco mosaic virus*, we refer to Stringlis et al. (2019) for an in-depth review about this topic. Remarkably, other beneficial microbes, like the induced systemic resistance (ISR) -inducing *Pseudomonas* strains *Pseudomonas simiae* WCS417 (hereafter; WCS417), *Pseudomonas putida* WCS358 (hereafter; WCS358) and the AM fungus *Rhizophagus irregularis* stand unaffected (Cosme et al., 2021; Stassen et al., 2021; Stringlis, De Jonge, et al., 2019), illustrating the nuanced specificity of coumarin mediated plant signaling. Recent research showed that the coumarin biosynthesis genes *MYB72* and *F6'H1* are required in the formation of a soil-borne legacy against the downy mildew pathogen *Hyaloperonospora arabidopsidis* (Hpa), as these coumarin biosynthesis genes were responsible for changes in the rhizosphere microbiome. Surprisingly, upon Hpa infection, most coumarin levels showed a notable decline (Vismans et al., 2022). Thus, either allowing coumarin sensitive microbes to proliferate or these biosynthesis genes produce more unknown compounds both of which can influence the rhizosphere microbiome and have a pivotal role in the formation of a soil-borne legacy. Other examples include the recruitment of *Bacillus subtilis* FB17 via malic acid secretion (Rudrappa et al., 2008). Or *Pseudomonas* and *Sphingomonas* enrichment via long-chain fatty acids and amino acids, which also showed to be able to induce ISR (Wen et al., 2021). Both of which occur after infection with the foliar pathogen *Pseudomonas syringae* pv. *tomato* DC3000 (Pst). Benzoxazinoid secretion by maize roots can recruit the beneficial bacterium *Pseudomonas putida* KT2440 (Neal et al., 2012). Even the amino acid tryptophan is utilized as signaling compound by cucumber upon *Fusarium oxysporum* infection. Tryptophan in turn helps selecting for the beneficial bacteria *Bacillus amyloliquefaciens* SQR9 (Y. Liu et al., 2017).

### Volatile organic compounds

Upon pathogen infection or herbivory plants can also produce VOCs. Plants produce a vast array of different VOCs which can have many different functions. Even though the spectrum of VOC signaling is versatile, research mainly focusses on the long distance effects influencing natural enemies or neighboring plants. Herbivory-induced plant VOCs can act as toxin, functioning as direct defense against herbivores or attract natural enemies, a phenomenon which has been reported in more than 50 different plant species and attract a wide range of predators (Hammerbacher et al., 2019; Zitzelsberger & Buchbauer, 2015). Additionally, a recent study conducted by Lee Díaz et al. (2024) showed that herbivory-induced VOCs can even alter the microbial rhizosphere composition. Other

plant VOCs are reported to induce resistance against specific pathogens as reviewed by Hammerbacher et al. (2019). As mentioned earlier plant VOCs can signal other neighboring plants protecting them against pathogens via the induction of immune responses (Sharifi et al., 2018), and even reshape the rhizosphere microbiome in the process, so that rhizosphere microbiomes of neighboring plants are similar (Kong et al., 2021).

These examples of compounds used by plants to signal distress during pathogen infection underscore the intricate and dynamic nature of plant microbe interactions. While many studies focus on the effects of individual compounds, it is essential to realize that root exudates encompass a multitude of different compounds. Therefore, the complete profile of these root exudates ultimately dictates whether a microbe is enriched or depleted in the rhizosphere. Moreover, such specific profiles most likely result in the enrichment of a consortium of beneficial microbes. This complexity highlights the need for further research focused on identifying unknown pathogen induced signaling compounds and the synergistic effects these compounds have on the rhizosphere microbiome.

## Root colonization

Plant derived signals act as semiochemicals to most microbes, meaning they trigger microbial responses. After perception of the host signal, microbes in general will respond by moving towards the root and try to colonize it. Since, pathogens can benefit from such signals as well, beneficial microbes will produce their own signaling compounds. In the AM symbiosis strigolactones released by the plant can be recognized by the AMF, but also by the parasitic plant striga. Once strigolactones are detected, the AMF will respond by the induction of spore germination and hyphal growth which allow the AMF to reach and attach to the root surface, whereas striga will respond by seed germination (Boyno & Demir, 2022; Ho-Plágaro & García-Garrido, 2022). To respond to the pathogen induced plant signals mentioned before, microbes require mechanisms to facilitate this and localize the root surface.

### Microbial movement

Bacteria utilize chemotaxis to localize the root and move towards it. Chemotaxis is a highly conserved mechanism, which is present in most bacteria, and relies on specific sensors which can bind signaling molecules. The ligand binding domain of methyl-accepting chemotaxis proteins (MCPs) can bind specific chemoattractants. These chemoattractants are typically secreted by plant roots and form gradients towards the roots. Typical chemoattractants can be nutrient rich compounds which function as food source such as sugars or amino acids, or secondary metabolites used by plants as signaling compound. Once the chemoattractant is bound to the MCP a signaling cascade is induced, which ultimately causes the phosphorylation of a Che factor. In turn a phosphorylated Che factor can activate the flagellum motor, causing bacterial motility. The exact configuration of the ligand binding domain of the MCPs differs among bacterial species, allowing different bacteria to respond to different chemoattractants (Feng et al., 2021). Taking this into account it is logical that chemotaxis-related genes are enriched in rhizobacteria, and that disruption in the flagella biosynthesis has a negative impact on root colonization (Feng et al., 2021; Yu et al., 2021).

### Root attachment

Once at the root surface microbes can initiate root attachment which consist of two distinct stages; The first stage called primary attachment creates relative weak and temporary bonds. Interactions between root and bacterial cell surface molecules create bonds based on electrostatic- and Van der Waals forces and hydrophobic interactions (Y. Liu et al., 2024; Wheatley & Poole, 2018). Such weak



bonds are universal to all plant-microbe interactions. The second stage secondary attachment creates stronger permanent bonds universally relying on the formation of cellulose fibrils which cover the cell surface and can tightly bind bacterial cells to root hairs (Y. Liu et al., 2024; Wheatley & Poole, 2018). The universally formed primary bonds are, as mentioned before, weak and due to the net negative charge of the bacterial cell surface, bacteria still tend to be repulsed from the root surface (Y. Liu et al., 2024). Therefore bacteria, dependent on the species, utilize a broad range of flagellum, adhesive pili, surface proteins and polysaccharides in primary attachment. For instance the genus *Rhizobium* utilize the surface polysaccharide glucomannan to bind to lectins on the root surface or use the extracellular protein rhicadhesin to form calcium based bonds these strategies are dependent on the soil pH. A combination of adhesive pili, rhicadhesion and Ti plasmids are used by *Agrobacterium* genus. Whereas, the outer membrane porin F (OprF), type IV pili and polysaccharides can be utilized by *Pseudomonas* species as adhesion factors (Y. Liu et al., 2024; Wheatley & Poole, 2018). Primary attachment is, in most cases, followed by secondary attachment which creates an irreversible bond between microbial and plant surfaces, allowing bacterial biofilms to form. As mentioned secondary attachment uses universal cellulose fibrils to realize such bonds. However, just like in primary attachment secondary attachment also uses species specific binding factors. For instance, *Pseudomonas* species utilize a calcium binding protein LapA, *Azospirillum* relies on the O-antigen within their lipopolysaccharide membrane and *Agrobacterium* uses unipolar polysaccharide (UPP) adhesion to facilitate binding to the root surface (Wheatley & Poole, 2018). It is worth noting that the given examples of factors used in primary and secondary attachment are just the tip of the iceberg. The bacterial kingdom is extremely diverse resulting in many different mechanisms which can be utilized in order to facilitate root attachment between plant and microbe. For a more complete overview regarding primary and secondary attachment we refer to several review papers covering these topics (Knights et al., 2021; Y. Liu et al., 2024; Wheatley & Poole, 2018). Furthermore, it is worth mentioning that biofilm formation can be promoted by the plants. A recent study showed that the root secreted VOC, MeJA, caused an increase in biofilm formation (Kulkarni et al., 2024).

Thus, the microbial response to plant signals is a multifaceted process governed by a variety of molecular mechanisms. Microbes showed to respond to host signals and employ chemotaxis to localize the root surface, where they initiate attachment, typically in two distinct stages, for which they utilize a diverse array of specialized adhesions factors. Mechanisms like chemotaxis, root binding and biofilm formation are, however, utilized by almost all microbes including pathogenic microbes. Nevertheless, beneficial microbes still need such mechanisms to initiate a symbiotic relationship with the host plant, they however, also need be able to distinguish themselves from their pathogenic counterparts.

## Beneficial microbe signaling

Upon detection of plant signals beneficial microbes will produce signaling compounds of their own. Such signaling compounds have a variety of functions and allow the host plant to recognize beneficial microbes as friendly. Upon detection of strigolactones AMF produce so called Myc factors, diffusible signals which cause transcriptional changes in the host plant and are required for AM establishment (Boyno & Demir, 2022; Ho-Plágaro & García-Garrido, 2022). Another critical step includes the evasion or suppression of plant immune responses. Central to such evasion and suppression tactics are the secretion of effector proteins, which have the potential to disrupt the plant's defense pathways but are not reserved for beneficial microbes (Boyno & Demir, 2022; Ho-Plágaro & García-Garrido, 2022; Pieterse et al., 2012). Studies predict that AMF have an arsenal of over 300 different effector proteins, of which only a small fraction is discovered. Among these known effectors are, SP7 which is

capable of inhibiting ethylene defense signaling, RiLSM which can bind to fungal chitin, making it undetectable by the plant's surveillance system and RiNLE1 which takes a more direct approach in immune suppression, inhibiting the expression of defense related genes in the host-plant as reviewed by Aparicio Chacón et al. (2023). Here we will go over the signaling tactics employed by beneficial microbes.

## Microbial symbiotic signaling

Similar to the Myc factors produced by AMF, beneficial *Rhizobia* produce Nod factors as signaling compounds essential for establishing successful symbiosis with leguminous plants. These Nod factors trigger plant responses necessary for initiating the symbiotic relationship. Specifically, Nod factors induce the formation of root nodules, specialized structures where nitrogen fixation takes place, thus facilitating the mutualistic interaction between the plant and bacteria (Boyno & Demir, 2022). Both, Myc and Nod factors are lipo-chitooligosaccharides (LCOs), characterized by their N-acetylglucosamine backbone and various additional modifications that tailor their function and specificity (Boyno & Demir, 2022). Interestingly, studies have revealed that pathogenic fungi can also produce LCOs, indicating that these molecules are not exclusive to mutualistic symbionts (Rush et al., 2020). Consequently, it is not surprising that plants contain numerous receptors that can bind specific LCOs (Thoms et al., 2021). It is postulated that this diversity in plant receptors allow plants to assess multiple molecular characteristics enhancing their ability to form beneficial associations while defending against potential pathogens. While it is tempting to speculate that other beneficial microbes might use similar signaling compounds, there is currently no evidence to support this hypothesis.

## Evading the plant immune system

What we do know is that some other, beneficial, microbes employ sophisticated strategies to prevent detection by the plants PRRs, thereby avoiding induction of MAMP triggered immunity (MTI) that could affect them. One used tactic involves the downregulation MAMP biosynthesis genes, for instance the downregulation of flagella biosynthesis as recently discovered for the for the ISR-inducing WCS417 (Yu et al., 2021). WCS417, along with its close relative WCS358, are known to produce VOCs upon root colonization. These bacterial VOCs induce the expression of *MYB72*, a key regulator of ISR (Zamioudis et al., 2015). However, in the process *MYB72* also induces the expression of the coumarin biosynthesis gene *F6'H1* (Stringlis et al., 2018). Interestingly, a transcriptome study revealed that WCS417 flagella biosynthesis genes are downregulated in *F6'H1* dependent manner, suggesting that WCS417 evolved a sophisticated tradeoff mechanism (Yu et al., 2021). By limiting the expression of flagella, WCS417 may evade plant immunity, without affecting its root colonization capabilities. Other rhizobacteria might rely on mutations within the conserved 22 amino acid sequence of the flg22 peptide, a key component of bacterial flagellin recognized by plant PRRs (Trdá et al., 2014). Furthermore, it is postulated that bacteria may use phase variation as a means of evading plant immune responses. This process allows bacteria to quickly switch between phenotypes, such as a phenotype with reduced flagellin biosynthesis, thereby altering their surface features and evade detection of the plant immune system (Martínez-Granero et al., 2014; Zamioudis & Pieterse, 2012).

## Suppression of the plant immune system

Another tactic used by rhizosphere inhabitants involves the direct suppression of plant immune responses, often achieved through the secretion of effector proteins that disrupt defense signaling pathways within plants. To deliver these effector proteins into the environment or host cells, beneficial rhizobacteria employ a variety of different secretion systems, with the type III secretion

system (T3SS) being among the most extensively studied. The T3SS enables bacteria to inject effector proteins directly into host cells, modulating plant immune responses and promoting microbial colonization. Studies revealed that a significant proportion of the beneficial bacteria found in the rhizosphere harbor genes encoding for the T3SS (Yu, Pieterse, et al., 2019). T3SS occasionally show to be required in plant-microbe interaction (Songwattana et al., 2021; Zamioudis & Pieterse, 2012), highlighting its widespread occurrence, and potential significance in plant-microbe interactions. For other plant beneficials strains like WCS417 and WCS374 genes have been found to encode numerous effector proteins, with WCS417 alone potentially producing up to 15 different effectors. While the specific functions of these proteins remain largely unknown, research has identified RopE, an effector protein from WCS417 with close resemblance to AvrE produced by *Pseudomonas syringae*. AvrE, and potentially RopE, have been shown to induce salicylic acid (SA) regulated defense responses in plants (Stringlis, Zamioudis, et al., 2019). Moreover, some *Pseudomonas* species have been observed to produce and secrete gluconic acid as a mechanism to acidify the soil surrounding plant roots. This acidification reduces the activation of root immune responses by flagellin derived peptide flg22, thereby promoting colonization of these *Pseudomonas* species (Yu, Liu, et al., 2019). Other species like *B. amyloliquefaciens* rely on VOCs. The VOC, diacetyl is used to counter the effects of a plant reactive oxygen species (ROS) burst (Morcillo et al., 2020).

## Hormonal crosstalk

In addition to examples of microbes evading or suppressing the plant's immune system, there are also examples where microbes manipulate hormonal crosstalk in plants. Hormonal crosstalk refers to the intricate interplay between plant hormones. Microbes can manipulate this balance to affect various traits like plant growth or defense. For instance a study in *Arabidopsis* has demonstrated that activation of the plant's immune system by the beneficial bacteria *Bacillus velezensis* FZB42 leads to the production of ROS. Interestingly, in order to counter the effects of the ROS burst, *B. velezensis* responds by inducing bacterial auxin production. In turn bacterial auxin enhances root colonization and triggers further plant immune responses. This dynamic interplay ultimately results in improved plant defense against fungal infection (Tzipilevich et al., 2021). Similarly, beneficial *Trichoderma* species have been shown to induce the production of jasmonic acid (JA) in plants, leading to the downregulation of defense genes that would otherwise restrict *Trichoderma* root colonization (Brotman et al., 2013). Additionally, *Sinorhizobium (Ensifer) Fredii* has been found to induce the suppression of SA in soybean, facilitating its own colonization on the root surface (Jiménez-Guerrero et al., 2015).

The ability to evade or suppress the plant immune responses is widespread among beneficial and pathogenic microbes alike, underscoring its critical role in successful root colonization. The interactions between host plant and microbes are mediated by a range of tactics, including the downregulation or modification of MAMPs and the secretion of various effector proteins which may or may not affect hormonal crosstalk. Additionally, research should point out whether signaling compounds produced by beneficial microbes are universally used in symbiotic interactions by means of discriminating between good and bad.

## Conclusion and future perspectives

This literature review aimed to elucidate the current understanding of the pathogen mediated "cry for help". We explored the mechanisms by which plants detect pathogen attacks and subsequently aim to recruit beneficial microbes. As well as the tactics employed by microbes to initiate successful symbiosis. Despite significant advancements in identifying the steps involved in these processes,

some critical details still remain elusive. One of the major gaps in our knowledge is how plants are able to discriminate between potential beneficial microbes or harmful pathogens. Current research suggests that plant recognition of variable MAMPs, such as LCOs, play key roles in this discrimination process, as these are involved in the *Rhizobia* and AM symbioses. It remains to be investigated whether this is a conserved mechanism in plant microbe interactions or if this is only reserved for these specific symbiotic interactions. Similarly, the selectiveness underlying the pathogen induced plant signaling compounds warrants further investigation. Understanding mechanisms that govern the specificity between host plants and beneficial microbes is crucial, especially in natural settings where plants secrete a multitude of compounds that can be perceived by a diverse array of microbes. Our understanding of plant microbe interactions holds significant promise for sustainable agricultural applications. By uncovering the detailed pathways and interactions, we can develop strategies that enhance crop resilience, growth and yield. Continued research in this field is essential for translating these insight into practical applications. In conclusion, while substantial progress has been made in decoding the pathogen induced “cry for help”, important questions remain unanswered. Future research uncovering these complex interactions can prove important for optimizing plant health and productivity.

## Bibliography

- Anzuay, M. S., Ludueña, L. M., Angelini, J. G., Fabra, A., & Taurian, T. (2015). Beneficial effects of native phosphate solubilizing bacteria on peanut (*Arachis hypogaea* L) growth and phosphorus acquisition. *Symbiosis*, *66*(2), 89–97. <https://doi.org/10.1007/s13199-015-0337-z>
- Aparicio Chacón, M. V., Van Dingenen, J., & Goormachtig, S. (2023). Characterization of Arbuscular Mycorrhizal Effector Proteins. In *International Journal of Molecular Sciences* (Vol. 24, Issue 11). Multidisciplinary Digital Publishing Institute (MDPI). <https://doi.org/10.3390/ijms24119125>
- Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S., & Vivanco, J. M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology*, *57*, 233–266. <https://doi.org/10.1146/annurev.arplant.57.032905.105159>
- Bakker, P. A. H. M., Berendsen, R. L., Doornbos, R. F., Wintermans, P. C. A., & Pieterse, C. M. J. (2013). The rhizosphere revisited: root microbiomics. *Frontiers in Plant Science*, *4*, 1–7. <https://doi.org/10.3389/fpls.2013.00165>
- Bakker, P. A. H. M., Pieterse, C. M. J., de Jonge, R., & Berendsen, R. L. (2018). The Soil-Borne Legacy. In *Cell* (Vol. 172, Issue 6, pp. 1178–1180). Cell Press. <https://doi.org/10.1016/j.cell.2018.02.024>
- Boyno, G., & Demir, S. (2022). Plant-mycorrhiza communication and mycorrhizae in inter-plant communication. In *Symbiosis* (Vol. 86, Issue 2, pp. 155–168). Springer Science and Business Media B.V. <https://doi.org/10.1007/s13199-022-00837-0>
- Brotman, Y., Landau, U., Cuadros-Inostroza, Á., Takayuki, T., Fernie, A. R., Chet, I., Viterbo, A., & Willmitzer, L. (2013). Trichoderma-Plant Root Colonization: Escaping Early Plant Defense Responses and Activation of the Antioxidant Machinery for Saline Stress Tolerance. *PLoS Pathogens*, *9*(3). <https://doi.org/10.1371/journal.ppat.1003221>
- Cosme, M., Fernández, I., Declerck, S., van der Heijden, M. G. A., & Pieterse, C. M. J. (2021). A coumarin exudation pathway mitigates arbuscular mycorrhizal incompatibility in *Arabidopsis thaliana*. *Plant Molecular Biology*, *106*(4–5), 319–334. <https://doi.org/10.1007/s11103-021-01143-x>

- Das, P. P., Singh, K. R., Nagpure, G., Mansoori, A., Singh, R. P., Ghazi, I. A., Kumar, A., & Singh, J. (2022). Plant-soil-microbes: A tripartite interaction for nutrient acquisition and better plant growth for sustainable agricultural practices. *Environmental Research*, 214. <https://doi.org/10.1016/j.envres.2022.113821>
- Dey, M., & Ghosh, S. (2022). Arbuscular mycorrhizae in plant immunity and crop pathogen control. In *Rhizosphere* (Vol. 22). Elsevier B.V. <https://doi.org/10.1016/j.rhisph.2022.100524>
- Feng, H., Fu, R., Hou, X., Lv, Y., Zhang, N., Liu, Y., Xu, Z., Miao, Y., Krell, T., Shen, Q., & Zhang, R. (2021). Chemotaxis of beneficial rhizobacteria to root exudates: The first step towards root–microbe rhizosphere interactions. *International Journal of Molecular Sciences*, 22(13). <https://doi.org/10.3390/ijms22136655>
- Gao, B., Chai, X., Huang, Y., Wang, X., Han, Z., Xu, X., Wu, T., Zhang, X., & Wang, Y. (2022). Siderophore production in pseudomonas SP. strain SP3 enhances iron acquisition in apple rootstock. *Journal of Applied Microbiology*, 133(2), 720–732. <https://doi.org/10.1111/jam.15591>
- Hamid, S., Lone, R., & Mohamed, H. I. (2021). Production of Antibiotics from PGPR and Their Role in Biocontrol of Plant Diseases. In H. I. Mohamed, H. ED. S. El-Beltagi, & K. A. Abd-Elsalam (Eds.), *Plant Growth-Promoting Microbes for Sustainable Biotic and Abiotic Stress Management*. Springer. [https://doi.org/https://doi.org/10.1007/978-3-030-66587-6\\_16](https://doi.org/https://doi.org/10.1007/978-3-030-66587-6_16)
- Hammerbacher, A., Coutinho, T. A., & Gershenzon, J. (2019). Roles of plant volatiles in defence against microbial pathogens and microbial exploitation of volatiles. In *Plant Cell and Environment* (Vol. 42, Issue 10, pp. 2827–2843). Blackwell Publishing Ltd. <https://doi.org/10.1111/pce.13602>
- Ho-Plágaro, T., & García-Garrido, J. M. (2022). Molecular Regulation of Arbuscular Mycorrhizal Symbiosis. In *International Journal of Molecular Sciences* (Vol. 23, Issue 11). MDPI. <https://doi.org/10.3390/ijms23115960>
- Jiménez-Guerrero, I., Pérez-Montaña, F., Monreal, J. A., Preston, G. M., Fones, H., Vioque, B., Ollero, F. J., & López-Baena, F. J. (2015). The Sinorhizobium (Ensifer) fredii HH103 type 3 secretion system suppresses early defense responses to effectively nodulate soybean. *Molecular Plant-Microbe Interactions*, 28(7), 790–799. <https://doi.org/10.1094/MPMI-01-15-0020-R>
- Knights, H. E., Jorriin, B., Haskett, T. L., & Poole, P. S. (2021). Deciphering bacterial mechanisms of root colonization. In *Environmental Microbiology Reports* (Vol. 13, Issue 4, pp. 428–444). John Wiley and Sons Inc. <https://doi.org/10.1111/1758-2229.12934>
- Kong, H. G., Song, G. C., Sim, H. J., & Ryu, C. M. (2021). Achieving similar root microbiota composition in neighbouring plants through airborne signalling. *ISME Journal*, 15(2), 397–408. <https://doi.org/10.1038/s41396-020-00759-z>
- Kulkarni, O. S., Mazumder, M., Kini, S., Hill, E. D., Aow, J. S. B., Phua, S. M. L., Elejalde, U., Kjelleberg, S., & Swarup, S. (2024). Volatile methyl jasmonate from roots triggers host-beneficial soil microbiome biofilms. *Nature Chemical Biology*, 20(4), 473–483. <https://doi.org/10.1038/s41589-023-01462-8>
- Lee Díaz, A. S., Minchev, Z., Raaijmakers, J. M., Pozo, M. J., & Garbeva, P. (2024). Impact of bacterial and fungal inoculants on the resident rhizosphere microbiome and the volatilome of tomato plants under leaf herbivory stress. *FEMS Microbiology Ecology*, 100(2). <https://doi.org/10.1093/femsec/fiad160>

- Liu, H., Li, J., Carvalhais, L. C., Percy, C. D., Prakash Verma, J., Schenk, P. M., & Singh, B. K. (2021). Evidence for the plant recruitment of beneficial microbes to suppress soil-borne pathogens. *New Phytologist*, 229(5), 2873–2885. <https://doi.org/10.1111/nph.17057>
- Liu, Y., Chen, L., Wu, G., Feng, H., Zhang, G., Shen, Q., & Zhang, R. (2017). Identification of root-secreted compounds involved in the communication between cucumber, the beneficial bacillus amyloliquefaciens, and the soil-borne pathogen fusarium oxysporum. *Molecular Plant-Microbe Interactions*, 30(1), 53–62. <https://doi.org/10.1094/MPMI-07-16-0131-R>
- Liu, Y., Xu, Z., Chen, L., Xun, W., Shu, X., Chen, Y., Sun, X., Wang, Z., Ren, Y., Shen, Q., & Zhang, R. (2024). Root colonization by beneficial rhizobacteria. In *FEMS Microbiology Reviews* (Vol. 48, Issue 1). Oxford University Press. <https://doi.org/10.1093/femsre/fuad066>
- Lugtenberg, B., & Kamilova, F. (2009). Plant-growth-promoting rhizobacteria. *Annual Review of Microbiology*, 63, 541–556. <https://doi.org/10.1146/annurev.micro.62.081307.162918>
- Martínez-Granero, F., Redondo-Nieto, M., Martín, M., & Rivilla, R. (2014). Phase Variation in Plant-Associated Pseudomonads. In: Katsy, E. (eds) *Plasticity in Plant-Growth-Promoting and Phytopathogenic Bacteria*. Springer.
- Morcillo, R. J., Singh, S. K., He, D., An, G., Vílchez, J. I., Tang, K., Yuan, F., Sun, Y., Shao, C., Zhang, S., Yang, Y., Liu, X., Dang, Y., Wang, W., Gao, J., Huang, W., Lei, M., Song, C., Zhu, J., ... Zhang, H. (2020). Rhizobacterium-derived diacetyl modulates plant immunity in a phosphate-dependent manner. *The EMBO Journal*, 39(2). <https://doi.org/10.15252/embj.2019102602>
- Muthuraja, R., & Muthukumar, T. (2021). Isolation and characterization of potassium solubilizing Aspergillus species isolated from saxum habitats and their effect on maize growth in different soil types. *Geomicrobiology Journal*, 38(8), 672–685. <https://doi.org/10.1080/01490451.2021.1928800>
- Naing, A. H., Maung, T. T., & Kim, C. K. (2021). The ACC deaminase-producing plant growth-promoting bacteria: Influences of bacterial strains and ACC deaminase activities in plant tolerance to abiotic stress. In *Physiologia Plantarum* (Vol. 173, Issue 4, pp. 1992–2012). John Wiley and Sons Inc. <https://doi.org/10.1111/ppl.13545>
- Neal, A. L., Ahmad, S., Gordon-Weeks, R., & Ton, J. (2012). Benzoxazinoids in root exudates of maize attract pseudomonas putida to the rhizosphere. *PLoS ONE*, 7(4). <https://doi.org/10.1371/journal.pone.0035498>
- Olanrewaju, O. S., Glick, B. R., & Babalola, O. O. (2017). Mechanisms of action of plant growth promoting bacteria. In *World Journal of Microbiology and Biotechnology* (Vol. 33, Issue 11). Springer Netherlands. <https://doi.org/10.1007/s11274-017-2364-9>
- Pantoja-Guerra, M., Burkett-Cadena, M., Cadena, J., Dunlap, C. A., & Ramírez, C. A. (2023). Lysinibacillus spp.: an IAA-producing endospore forming-bacteria that promotes plant growth. *Antonie van Leeuwenhoek, International Journal of General and Molecular Microbiology*, 116(7), 615–630. <https://doi.org/10.1007/s10482-023-01828-x>
- Pieterse, C. M. J., Van Der Does, D., Zamioudis, C., Leon-Reyes, A., & Van Wees, S. C. M. (2012). Hormonal modulation of plant immunity. *Annual Review of Cell and Developmental Biology*, 28, 489–521. <https://doi.org/10.1146/annurev-cellbio-092910-154055>

- Pieterse, C. M. J., Zamioudis, C., Berendsen, R. L., Weller, D. M., Van Wees, S. C. M., & Bakker, P. A. H. M. (2014). Induced systemic resistance by beneficial microbes. *Annual Review of Phytopathology*, *52*, 347–375. <https://doi.org/10.1146/annurev-phyto-082712-102340>
- Rudrappa, T., Czymmek, K. J., Paré, P. W., & Bais, H. P. (2008). Root-secreted malic acid recruits beneficial soil bacteria. *Plant Physiology*, *148*(3), 1547–1556. <https://doi.org/10.1104/pp.108.127613>
- Rush, T. A., Puech-Pagès, V., Bascaules, A., Jargeat, P., Maillet, F., Haouy, A., Maès, A. Q. M., Carriel, C. C., Khokhani, D., Keller-Pearson, M., Tannous, J., Cope, K. R., Garcia, K., Maeda, J., Johnson, C., Kleven, B., Choudhury, Q. J., Labbé, J., Swift, C., ... Ané, J. M. (2020). Lipo-chitooligosaccharides as regulatory signals of fungal growth and development. *Nature Communications*, *11*(1). <https://doi.org/10.1038/s41467-020-17615-5>
- Sharifi, R., Lee, S. M., & Ryu, C. M. (2018). Microbe-induced plant volatiles. In *New Phytologist* (Vol. 220, Issue 3, pp. 684–691). Blackwell Publishing Ltd. <https://doi.org/10.1111/nph.14955>
- Song, Y., & Haney, C. H. (2021). Drought dampens microbiome development. In *Nature Plants* (Vol. 7, Issue 8, pp. 994–995). Nature Research. <https://doi.org/10.1038/s41477-021-00977-z>
- Songwattana, P., Chaintreuil, C., Wongdee, J., Teulet, A., Mbaye, M., Piromyou, P., Gully, D., Fardoux, J., Zoumman, A. M. A., Camuel, A., Tittabutr, P., Teaumroong, N., & Giraud, E. (2021). Identification of type III effectors modulating the symbiotic properties of *Bradyrhizobium vignae* strain ORS3257 with various *Vigna* species. *Scientific Reports*, *11*(1). <https://doi.org/10.1038/s41598-021-84205-w>
- Stassen, M. J. J., Hsu, S. H., Pieterse, C. M. J., & Stringlis, I. A. (2021). Coumarin Communication Along the Microbiome–Root–Shoot Axis. *Trends in Plant Science*, *26*(2), 169–183. <https://doi.org/10.1016/j.tplants.2020.09.008>
- Stringlis, I. A., De Jonge, R., & Pieterse, C. M. J. (2019). The age of coumarins in plant-microbe interactions. *Plant and Cell Physiology*, *60*, 1405–1419. <https://doi.org/10.1093/pcp/pcz076>
- Stringlis, I. A., Yu, K., Feussner, K., De Jonge, R., Van Bentum, S., Van Verk, M. C., Berendsen, R. L., Bakker, P. A. H. M., Feussner, I., & Pieterse, C. M. J. (2018). MYB72-dependent coumarin exudation shapes root microbiome assembly to promote plant health. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, E5213–E5222. <https://doi.org/10.1073/pnas.1722335115>
- Stringlis, I. A., Zamioudis, C., Berendsen, R. L., Bakker, P. A. H. M., & Pieterse, C. M. J. (2019). Type III secretion system of beneficial rhizobacteria *Pseudomonas simiae* WCS417 and *Pseudomonas defensor* WCS374. *Frontiers in Microbiology*, *10*(JULY). <https://doi.org/10.3389/fmicb.2019.01631>
- Sun, K., Xie, X. G., Lu, F., Zhang, F. M., Zhang, W., He, W., & Dai, C. C. (2021). Peanut preinoculation with a root endophyte induces plant resistance to soil-borne pathogen *Fusarium oxysporum* via activation of salicylic acid-dependent signaling. *Plant and Soil*, *460*(1–2), 297–312. <https://doi.org/10.1007/s11104-020-04807-7>
- Tao, J., Gu, M., Yu, S., Shi, J., Cheng, L., Jin, J., Lu, P., Zhang, J., Li, H., & Cao, P. (2024). The beneficial endophytic microbes enhanced tobacco defense system to resist bacterial wilt disease. *Chemical and Biological Technologies in Agriculture*, *11*(1). <https://doi.org/10.1186/s40538-024-00542-8>

- Thoms, D., Liang, Y., & Haney, C. H. (2021). Maintaining symbiotic homeostasis: How do plants engage with beneficial microorganisms while at the same time restricting pathogens? In *Molecular Plant-Microbe Interactions* (Vol. 34, Issue 5, pp. 462–469). American Phytopathological Society. <https://doi.org/10.1094/MPMI-11-20-0318-FI>
- Trdá, L., Fernandez, O., Boutrot, F., Héloir, M. C., Kelloniemi, J., Daire, X., Adrian, M., Clément, C., Zipfel, C., Dorey, S., & Poinssot, B. (2014). The grapevine flagellin receptor VvFLS2 differentially recognizes flagellin-derived epitopes from the endophytic growth-promoting bacterium *Burkholderia phytofirmans* and plant pathogenic bacteria. *New Phytologist*, *201*(4), 1371–1384. <https://doi.org/10.1111/nph.12592>
- Tsukanova, K. A., Chebotar, V., Meyer, J. J. M., & Bibikova, T. N. (2017). Effect of plant growth-promoting Rhizobacteria on plant hormone homeostasis. In *South African Journal of Botany* (Vol. 113, pp. 91–102). Elsevier B.V. <https://doi.org/10.1016/j.sajb.2017.07.007>
- Tzipilevich, E., Russ, D., Dangl, J. L., & Benfey, P. N. (2021). Plant immune system activation is necessary for efficient root colonization by auxin-secreting beneficial bacteria. *Cell Host and Microbe*, *29*(10), 1507-1520.e4. <https://doi.org/10.1016/j.chom.2021.09.005>
- Vismans, G., van Bentum, S., Spooren, J., Song, Y., Goossens, P., Valls, J., Snoek, B. L., Thiombiano, B., Schilder, M., Dong, L., Bouwmeester, H. J., Pétriaccq, P., Pieterse, C. M. J., Bakker, P. A. H. M., & Berendsen, R. L. (2022). Coumarin biosynthesis genes are required after foliar pathogen infection for the creation of a microbial soil-borne legacy that primes plants for SA-dependent defenses. *Scientific Reports*, *12*(1). <https://doi.org/10.1038/s41598-022-26551-x>
- Wang, B., Zhang, Z., Xu, F., Yang, Z., Li, Z., Shen, D., Wang, L., Wu, H., Li, T., Yan, Q., Wei, Q., Shao, X., & Qian, G. (2023). Soil bacterium manipulates antifungal weapons by sensing intracellular type IVA secretion system effectors of a competitor. *ISME Journal*, *17*(12), 2232–2246. <https://doi.org/10.1038/s41396-023-01533-7>
- Wang, N. R., & Haney, C. H. (2020). Harnessing the genetic potential of the plant microbiome The plant microbiome expands the genetic potential of plants. *The Biochemist*, *42*(4), 20–25. <http://portlandpress.com/biochemist/article-pdf/42/4/20/891009/bio20200042.pdf>
- Wang, S., Fan, H., Zhao, D., Zhu, X., Wang, Y., Liu, X., Liu, D., Duan, Y., & Chen, L. (2021). Multifunctional efficacy of the nodule endophyte *Pseudomonas fragi* in stimulating tomato immune response against *Meloidogyne incognita*. *Biological Control*, *164*. <https://doi.org/10.1016/j.biocontrol.2021.104773>
- Wen, T., Zhao, M., Yuan, J., Kowalchuk, G. A., & Shen, Q. (2021). Root exudates mediate plant defense against foliar pathogens by recruiting beneficial microbes. *Soil Ecology Letters*, *3*(1), 42–51. <https://doi.org/10.1007/s42832-020-0057-z>
- Wheatley, R. M., & Poole, P. S. (2018). Mechanisms of bacterial attachment to roots. In *FEMS Microbiology Reviews* (Vol. 42, Issue 4, pp. 448–461). Oxford University Press. <https://doi.org/10.1093/femsre/fuy014>
- Yu, K., Liu, Y., Tichelaar, R., Savant, N., Lagendijk, E., van Kuijk, S. J. L., Stringlis, I. A., van Dijken, A. J. H., Pieterse, C. M. J., Bakker, P. A. H. M., Haney, C. H., & Berendsen, R. L. (2019). Rhizosphere-associated *Pseudomonas* suppress local root immune responses by gluconic acid-mediated lowering of environmental pH. *Current Biology*, *29*, 3913-3920.e4. <https://doi.org/10.1016/j.cub.2019.09.015>



- Yu, K., Pieterse, C. M. J., Bakker, P. A. H. M., & Berendsen, R. L. (2019). Beneficial microbes going underground of root immunity. In *Plant Cell and Environment* (Vol. 42, Issue 10, pp. 2860–2870). Blackwell Publishing Ltd. <https://doi.org/10.1111/pce.13632>
- Yu, K., Stringlis, I. A., van Bentum, S., de Jonge, R., Snoek, B. L., Pieterse, C. M. J., Bakker, P. A. H. M., & Berendsen, R. L. (2021). Transcriptome signatures in *Pseudomonas simiae* WCS417 shed light on role of root-secreted coumarins in Arabidopsis-mutualist communication. *Microorganisms*, *9*(3), 1–15. <https://doi.org/10.3390/microorganisms9030575>
- Yue, Z., Chen, Y., Hao, Y., Wang, C., Zhang, Z., Chen, C., Liu, H., Liu, Y., Li, L., & Sun, Z. (2022). *Bacillus* sp. WR12 alleviates iron deficiency in wheat via enhancing siderophore- and phenol-mediated iron acquisition in roots. *Plant and Soil*, *471*(1–2), 247–260. <https://doi.org/10.1007/s11104-021-05218-y>
- Zaheer, M. S., Ali, H. H., Iqbal, M. A., Erinle, K. O., Javed, T., Iqbal, J., Hashmi, M. I. U., Mumtaz, M. Z., Salama, E. A. A., Kalaji, H. M., Wróbel, J., & Dessoky, E. S. (2022). Cytokinin Production by *Azospirillum brasilense* Contributes to Increase in Growth, Yield, Antioxidant, and Physiological Systems of Wheat (*Triticum aestivum* L.). *Frontiers in Microbiology*, *13*. <https://doi.org/10.3389/fmicb.2022.886041>
- Zamioudis, C., Korteland, J., Van Pelt, J. A., Van Hamersveld, M., Dombrowski, N., Bai, Y., Hanson, J., Van Verk, M. C., Ling, H. Q., Schulze-Lefert, P., & Pieterse, C. M. J. (2015). Rhizobacterial volatiles and photosynthesis-related signals coordinate MYB72 expression in Arabidopsis roots during onset of induced systemic resistance and iron-deficiency responses. *The Plant Journal*, *84*, 309–322. <https://doi.org/10.1111/tpj.12995>
- Zamioudis, C., & Pieterse, C. M. J. (2012). Modulation of host immunity by beneficial microbes. *Molecular Plant-Microbe Interactions*, *25*, 139–150. <https://doi.org/10.1094/MPMI-06-11-0179>
- Zitzelsberger, C., & Buchbauer, G. (2015). Essential Oils as “A Cry for Help”. A Review. *Natural Product Communications*, *10*(6).