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The impact of defense hormones on the interaction between plants and the soil microbial community

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Chapter 6

General discussion

General discussion

Plants can alter the microbial community in their rhizosphere, and in turn, the microbial community influences plant growth and development (Bever 1994; van der Heijden et al., 2008; Hahl et al., 2020). In general, the relationship between plants and soil microbes can be neutral, positive and negative (Nijjer et al., 2007; Bhattacharyya and Jha, 2012). However, often plants grow less well in soil that contains a live microbial community (live soil) than when growing in sterilized soil (Kulmatiski et al., 2008). An overall net effect of soil microbial pathogenic microbes is one of the many mechanisms behind reduced plant growth in live soils (Cesarano et al., 2017).

In nature, plants have developed many defensive strategies, e.g. via hormone signaling, against microbial pathogens or herbivores. In agriculture, inducing hormonal signaling pathways has become a promising strategy to increase plant resistance against these enemies (Haney and Ausubel, 2015; Yang et al., 2015), and this is now applied to control soil microbial pathogens (Fujita et al., 2006; Yang et al., 2015; Berens et al., 2019). Exogenous application of SA to plant leaves activates systemic acquired resistance in the plant associated with the production of pathogen-related proteins against microbial pathogens (Reymond and Farmer, 1998), while foliar application of JA or MeJA activates induced systemic defenses against herbivores and necrotrophic pathogens (Nahar et al., 2011). If the reduction of plant growth in live soil is caused by an overall pathogenic effect from the soil microbial community, we would expect that plant defense signaling hormones play a role in the interaction between the soil microbial community and plants. In particular, we would expect the negative effect to be mitigated after the application of SA as this would increase the defense of plants against microbes (Maurhofer et al., 1998; Berendsen et al., 2012; Wang et al., 2013).

Although a number of studies assessed the positive effects of hormonal signaling pathways on a plant's immunity against pathogenic microbes, whether and how these hormonal signaling pathways affect the soil microbial community and subsequently plant growth is still poorly understood, and whether activation of SA-induced resistance could potentially select a more beneficial soil microbial community over time is not known.

In this thesis, I examined how harnessing the plants' immune system affects the relationship between plants and the soil microbial community. I tested the hypothesis that the negative effect of live soil on plant growth is due to changes in the microbial community belowground and that activation of SA-induced resistance will potentially mitigate the negative effect of live soil on plant growth through altering the rhizosphere microbial composition and the expression of functional genes. Furthermore, I investigated how long-lasting the effect of the soil microbial community on plant growth is and if the effect changed at different plant growth stages.

In this chapter, I discuss the findings of this thesis and compare them with the results from several recently published studies in this research field, aiming to provide a broader perspective of my research findings within the field of above-belowground plant-soil interactions.

Activation of hormonal induced defenses in plants growing in live soil

Many plant species produce more biomass in sterilized soil than in soil that contains a live microbial community. This could be due to an overall net pathogenic effect of the soil microbial community (Kulmatiski et al., 2008; Miki 2012). In Chapter 2 I studied the effect of live soil on plant growth of four plant species to investigate whether the overall negative soil effect is a common phenomenon among these plant species. Interestingly, the live soil only negatively affected two (*J. vulgaris* and *C. vulgare*) out of the four tested plant species, while for the other two species (*T. repens* and *D. carota*) we found no effect. This finding is in line with previous studies showing that interactions between plant species and soil microbial communities are highly species-specific (Klironomos, 2002; Joosten et al., 2009; Harrison and Bardgett, 2010; Wang et al., 2019). Plant genotype, diversity and neighboring-species can all influence these interactions, and the soil microbial community (reviewed in Bever et al., 2010), and this effect is mostly likely related to secondary metabolites exuded by the plants (Smith et al., 2018; Zhu et al., 2019; Dror et al., 2020). For example, pyrrolizidine alkaloids (PAs) are a group of secondary metabolites of the species *J. vulgaris* that are known to affect soil microbial pathogens. Genotypes of *J. vulgaris* vary in the concentration of PAs that they contain and presumably exude, and

this can influence soil microbial communities (Kowalchuk et al., 2006; Joosten et al., 2009; Kirk et al., 2010; Kostenko et al., 2012). Other studies have shown that root-emitted volatile compounds influence the composition of soil microbial communities (Delory et al., 2016; Massalha et al., 2017; Bailly 2020).

In addition, I examined if the live soil effect can be altered by the foliar application of SA or JA. Overall, activation of hormonal-induced resistance itself for a plant is costly (Vos et al., 2013). This is exemplified in my work where the foliar application of JA and SA to plant leaves resulted in reduced plant growth when plants were grown in sterilized soil for all four species (Chapter 2). Notably, for the two species in which the live soil had a negative effect on plant growth, we found that this effect was mitigated by the application of SA. In the other two species, the application of SA did not affect plant growth. Plants respond to biotic stresses (i.e., microbial pathogens) through regulation of sophisticated hormonal signaling networks (Fujita et al., 2006; Arnaud and Hwang, 2015). In my study, induced plant defenses triggered by foliar application of the plant hormone SA mitigated the negative effect of live soil, while application of JA did not have a positive effect on plant growth in all treatments and all species. This is probably related to the functions of these hormones; SA-induced resistance targets microbial pathogens (Reymond and Farmer, 1998), while JA-induced resistance targets herbivores and necrotrophic pathogens (Nahar et al., 2011).

For *J. vulgaris*, we then continued by studying the effect of the live soil and SA application during four subsequent generations. The negative effect of the live soil was observed in all generations but did not increase or decline over time (Chapter 2). The mitigating effect of SA on the negative effects of the live soil on plant growth also did not change over generations. The reduced plant growth in live soils can be caused by nutrient competition between plants and soil microbes or by an overall pathogenic effect of soil microbial community (Hodge et al., 2013; Cesarano et al., 2017; Trivedi et al., 2020). However, in our experiment, we fertilized the plants and hence we expect that competition for nutrients was not important and that an overall microbial pathogenic effect is the most likely explanation for the plant growth reduction in live soil. Further, we hypothesized that we can select for a more beneficial community over time because the foliar application of SA mitigates the

negative live soil effect in *J. vulgaris* but we did not observe that the mitigating effect increased over generations.

Little is known about how such hormonal pathways affect the inoculated live soils and how this, in turn, impacts plant growth. Several studies argue that the ‘SA-mitigated effect’ can be due to (1) a boosted immune system in the plant itself (Chen et al., 2020; Koo et al., 2020), or (2) changes in the plant-microbes interaction (Nishad et al., 2020; Kumar 2020). However, evidence for the second hypothesis in soil environments is still contradictory. For instance, Berendsen et al. (2012) and Doornbos et al. (2011) demonstrated that activation of JA and SA signaling pathways did not affect the resident soil microflora, while a recent study showed that SA modulates colonization of the root microbiome by specific bacterial taxa (Lebeis et al., 2015). In our study, JA application did not affect the relationship between the soil microbial community and plant growth, and this indicates that in our experiments there was no strong cross-talk between SA and JA.

SA-induced defenses and soil microbial composition

Based on the results of Chapter 2 we studied if the SA-mitigated effect on the soil microbial community was accompanied by a shift in the composition of the microbial community. In Chapter 3, we studied the composition of the rhizosphere microbial community of *J. vulgaris* over four generations. We found that the composition of the soil microbial community in the rhizosphere soil changed across generations, but not in a consistent manner. This may have resulted from the experimental design that we selected. For each generation, we used an inoculum, which means that we placed a subset of the microbial community in a sterile background. This may explain why we saw so much variation temporally, as in each generation a different subset of the microbial community may have been activated.

Although we did find an overall effect of SA on the total microbial composition, the direction of these changes was different in each generation. Application of SA selected for different bacterial genera in the rhizosphere soil, but these selected genera differed from generation to generation. This suggests that the effects of SA application to plants on the soil microbial community are not consistent over time. It is also

possible that bacterial microbial community composition is variable over time (Gilbert et al., 2009; Hickey et al., 2013; Lauber et al., 2013; Hannula et al., 2019). The impact of SA-induced resistance on soil microbial communities is still debated. For example, Hein et al. (2008) found that SA-induced resistance in *Arabidopsis* mutants changed the structure of bacterial communities in the rhizosphere. Wang et al. (2015) and Doornbos et al. (2011) both demonstrated that activation of SA-induced resistance did not significantly affect the composition and diversity of the rhizosphere bacterial community. As the SA effect on the microbial composition varied from generation to generation, it is difficult to predict the effects of activation of plant defenses on soil microbes. This may also explain why there was no selection for more beneficial communities over generations.

Application of SA to plants significantly up-regulated genera of *Caballeronia*, unclassified *Cytophagaceae*, *Crinalium* and *Candidatus Thermofonsia Clade 2*, and down-regulated the genera of *Thermomicrobiales*, unclassified *Rhodobacterales*, *Paracoccus* and *Flaviumibacter*. While the functions of many of these bacteria are poorly understood, bacteria of the genus *Caballeronia* are often reported to play an important role in fixing nitrogen and promoting plant growth, and species in this genus are predominantly endophytic diazotrophic bacteria and N-fixing bacteria (Puri et al., 2018; Padma et al., 2018; Puri et al., 2020). Hence, this suggests that activation of the SA signaling pathway in *J. vulgaris* plants may select for bacterial genera that are beneficial to the plant.

SA-induced defenses and soil microbial functional genes

In Chapter 3, we analyzed the changes of microbial taxonomy in the rhizosphere soil and found that the effects of SA on the rhizosphere bacterial communities of *J. vulgaris* were inconsistent over generations. We hypothesized that we would see a common functional gene expression in the same soil samples, because the functions of the soil microbial community are often distributed across microbial taxa (Burke et al., 2011; Liu et al., 2018; Liu et al., 2020). One of the explanations can be that the composition of the soil microbial community shows a great redundancy concerning the functioning of microbial species and that changes in microbial diversity are not

always consistent with changes in functional gene expression in soil microbial communities.

In our study, we found that the functional genes of rhizosphere microbial communities of *J. vulgaris* were affected by the SA treatment, by generation and by the interplay between SA treatment and generation. However, none of the significantly SA-downregulated genes was present in all four generations, while only one SA-upregulated gene was observed in all four generations. To date, information about the effects of phytohormone application to plants on the functions of rhizosphere microbiomes are limited (Anderson et al., 2004; Carvalhais et al., 2013). To our knowledge, the work presented in this thesis is among the first to study how activation of SA induced resistance affects natural soil microbiomes at the functional gene level. SA induced resistance is often reported to play an important role in resistance to a broad range of microbial pathogens, such as bacteria, fungi and viruses. Concerning viruses, SA has been reported to act as an elicitor in various plant species, such as tobacco, cucumber, *Vigna mungo*, tomato, sugarcane (Murphy et al., 1999; Gilliland et al., 2003; Mayers et al., 2005; Kundu et al., 2011; Li et al., 2019; Yuan et al., 2019).

A limitation in the current work is that not all detected genes could be annotated with known functions. Interestingly, at a gene ontology level, we found that soil microbial communities in the rhizosphere soil of SA-treated plants utilized several gene ontology processes. For the increased GO terms, they were mostly related to viral RNA genome replication, to interactions with host cells, to organelles of the host cells and to RNA polymerase activities; while for the decreased GO terms, they were associated with processing nitrogen and macromolecules. However, it still remains unproven that if those processes are associated with infection processes of the host plant and are potentially linked to suppression of pathogenic infections. Interestingly, up-regulated GO terms that were involved in viral (RNA) genome replication and viral processes were frequently found in our study in the soil of SA-treated plants. As it is well-reported that viral-phage therapy uses viruses or bacteriophages to control pathogens. A viral phage first attaches to the surface of a pathogenic bacteria, then injects its genome into the cells, self-replicates in the bacteria, and eventually kills the bacteria by causing them to burst or lyse (Duckworth and Gulig, 2002; Svircev et al., 2018; Jamal et al., 2019; Kortright et al., 2019; Rehman et al., 2019). This has recently

been brought up as an alternative for the usage of pesticides to control bacterial pathogens in agriculture (Rehman et al., 2019). Therefore, it is important to note that virus-microbe-plant interactions should be taken into account in future studies.

Plant growth stages and negative plant-soil effects

In our experiments, we placed a subset of the microbial community in a sterile background and this may have led temporal variation in the soil microbial community in each generation. Most studies on plant-soil-interactions have examined the effect of the soil microbial community on plant mass after a fixed duration of plant growth (Smith and Reynolds, 2012; Hodge and Fitter 2013; Dudenhöffer et al., 2018). However, these interactions may change over time (Bezemer et al., 2018). In Chapter 5, we examined how long-lasting the effect of the soil microbial community on plant growth is and we established relative plant growth rates at different growth stages (early, mid and late plant growth).

We found in all experiments that we carried out to study these temporal effects, that differences in dry plant mass between the plants grown in sterilized soil and inoculated soil (live soil) increased over the course of the experiment. Interestingly, linear regression models with \ln transformed dry plant mass against time at the early stage and later stage in sterilized soil and live soil, respectively, showed that the relative growth rate of plants in the sterilized soil and live soil only differed in the first weeks and that there were no significant differences in relative growth rates during the late stage. Our study exemplifies that the negative effects of soil inoculation on plant mass can extend over the whole growth period, but that these differences are due to negative effects that occur in the first weeks after planting. This might be because younger plants or seedlings are more vulnerable and susceptible to pathogenic microbes in the soil than older plants with well-developed root systems (Packer and Clay, 2000). Root development plays an important role for plants in suppressing soil microbial pathogens (Watt et al., 2006; Emmett et al., 2014), and is often correlated with soil abiotic or biotic characteristics (Kardol et al., 2013; Arrigoni et al., 2018; Bezemer et al., 2018). Our findings are in line with previous work (Bezemer et al., 2018) on the same plant species, *J. vulgaris*, where seedlings were planted again in soil that had been conditioned by other plants of the same species.

Their findings show that the differences between responses of young and old plants are likely related to the sensitivity of plant stages and not due to temporal changes in the soil community.

Concluding remarks and future perspective

The outcomes of this thesis contribute to our understanding of how harnessing of the plant immune system affects the relationship between plants and the soil microbial community. From this work, we can conclude that the effect of live soil on plant growth is species-specific. Moreover, we conclude that application of SA can mitigate the negative effect of live soil on plant growth and we hypothesize that the negative effect of live soil on plant performance is driven by microbial pathogens in the soil. Further, from the multi-generational experiment, we conclude that activation of SA-associated plant defense pathways alters the composition of soil microbial communities of *J. vulgaris* but that these effects vary over time. We found no evidence that activation of SA signaling pathways in plants results in the selection of bacteria that are more beneficial to plant growth. The functions of the majority of the significantly affected genera by SA-induced resistance in our experiment are not well-known. SA-induced resistance, against soil microbial pathogens in *J. vulgaris* may be through the regulation of virus or viral related pathways. Last but not least, we concluded that negative effects of live soil on plant growth may appear consistent over time, but may only be caused by negative effects on plant growth that occur during the first few weeks. Overall, our study exemplifies that aboveground induction of plant defenses, can lead to complex above-belowground feedbacks.

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