Multidisciplinary approach to study effects of beneficial rhizobacteria on induced plant defences to abovegroung herbivorous insects

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PUBLISHABLE SUMMARY

Plants in nature interact with a wide range of above- and belowground organisms that have beneficial or detrimental effects on plant development. Plants have direct defences, such as toxins or thorns, to defend themselves against damaging insect herbivores. Additionally, plants have also developed indirect defences to promote the effectiveness of natural enemies of those insect herbivores, such as volatiles that plants produce in response to herbivory and that are used by the natural enemies of that herbivore as cues to find their prey. Belowground, plants establish mutualistic interactions with several beneficial microbes that live in the rhizosphere, such as mycorrhizal fungi and rhizobacteria, which can help plants to deal with different stresses. Since long, scientists know the beneficial effects of such microbes on promoting plant growth and controlling the growth of root pathogens. But recently, exciting discoveries show that the effects of soil microbes can cross the soil border and interact via changes in the plant, with herbivorous insects, their natural enemies, and pollinators aboveground. The role of these interactions in natural and agricultural ecosystems is receiving increased attention, but our understanding of the molecular and physiological mechanisms involved in these interactions is still in its infancy.

In this project, it has been investigated how beneficial rhizobacteria belowground affect direct defences aboveground against insect herbivores, as well as indirect defences to attract the natural enemies of those herbivores. This was evaluated in controlled conditions, using the model plant *Arabidopsis thaliana* and several strains of the rhizobacterium species *Pseudomonas fluorescens*. To determine the effects of rhizobacteria on herbivores, we assess the preference and performance of several species of generalist and specialist herbivores from two different feeding guilds (phloem feeders and leaf chewers). To determine the effect of rhizobacteria on indirect defences, the attraction of a natural enemy (parasitoid) of aphids (phloem feeder) was evaluated, and the associated changes in the emission of herbivore-induced plant volatiles.

The performance of specialist herbivores was not affected by the presence of rhizobacteria, probably due to a high adaptation of the herbivores to the toxins of their host plants. In contrast, rhizobacteria had a differential effect on generalist herbivores. Rhizobacteria induced systemic resistance against leaf chewers (the caterpillars *Spodoptera exigua* and *Mamestra brassicae*) whereas the colonization by rhizobacteria induced systemic susceptibility to phloem feeders (in this case the aphid *Myzus persicae*). Herbivore preference was not affected by the presence of rhizobacteria under the evaluated experimental conditions. At the molecular level in the plant, rhizobacteria enhanced the expression of defensive genes after attack by the generalist herbivores. However it seems that aphids could benefit from the enhanced plant nutrition triggered by rhizobacteria, whereas leaf chewers were more affected

by the induced resistance. The results on indirect defences, show that the volatile blend emitted by plants with and without rhizobacteria is different. However, in contrast to our expectations, parasitoids of phloem feeders are more attracted to plants without rhizobacteria. The colonization by rhizobacteria triggers a strong modification in the plant, and such modification interferes with the host recognition by aphid parasitoids.

These effects of rhizobacteria on herbivores are in line with the proposed pattern for other beneficial soil-borne microbes. Mutualistic soil-borne microbes have two main beneficial effects on plants: growth promotion and induced systemic resistance. Beneficial effects on plant growth have a high relevance for agricultural ecosystems since it reduces the need for fertilizers, leading to a decrease in pollution of agricultural soils and water. The mechanism of induced systemic resistance has been proven to protect many plant species against different attackers, therefore these microbes could be used as a promising strategy to control multiple pests, with the associated reduction on the use of chemical pesticides. However, we have proven in this project that a beneficial strategy against one type of attacker might not be effective against a different attacker. There is a high context-dependency on the effects of these beneficial microbes on herbivores, and more studies determining what is driving such dependency are needed.

Even if the direct and indirect defences fail and the herbivore pressure increases, soil-borne microbes can still enhance plant biomass and yield. These microbes have other beneficial effects for plants such as increased tolerance to environmental stresses, for instance nutrient deficiencies, drought or presence of heavy metals in the soil. Microbes may provide a promising contribution to sustainable pest control in a changing environment, through enhancing plant productivity, resistance to pathogens and pests, attractiveness to beneficial insects and tolerance to abiotic and biotic stress.