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Commentary

Transcript accumulation in a trifold interaction gives insight into mechanisms of biocontrol

Through their roots, plants interact with a highly complex community of bacteria, fungi, oomycetes and protozoa. Such rhizospheric interactions are thought to play an important role in plant performance, but current knowledge about mechanisms does not go much beyond bilateral interactions. Many of such studies showed that some rhizosphere microbes can be beneficial for nutrient uptake or disease resistance, whereas others are potential pathogens. Soil-borne pathogens are especially problematic for agriculture because once disease symptoms caused by such a pathogen become apparent there is no cure. Prophylactic soil treatment to prevent disease using chemicals or steam is expensive and has adverse effects on the environment including the rhizosphere microbiome.

'This constitutes an important step forward in identifying and untangling direct from indirect effects of biocontrol on the level of transcriptional responses.'

An alternative possibility to control diseases caused by soil-borne pathogens has emerged from the study of 'suppressive soils' in which biotic agents suppress disease despite the presence of a pathogen (Schlatter *et al.*, 2017). This phenomenon was termed biocontrol, and has now been demonstrated in a wide variety of crops (De Vrieze *et al.*, 2018; Newitt *et al.*, 2019). However, the mechanisms underlying biocontrol remain largely elusive. In general, both direct effects like competition or antibiosis and indirect effects like induced resistance have been observed and were analysed also on a molecular level (Köhl *et al.*, 2019). In some cases, biocontrol agents, pathogens and plants were combined in these analyses and important discoveries were made, such as the phenomenon of priming (Conrath *et al.*, 2006). In most studies however, one partner in the interaction was the focus of the investigation and the others were seen as 'treatments'. In this issue of *New Phytologist*, the group of Alga Zuccaro (Sarkar *et al.*, 2019; pp. 886–901) reports an analysis of the tripartite interaction between barley, the pathogenic fungus *Bipolaris sorokiniana* and the disease-suppressing endophytic fungus *Serendipita vermifera*.

This article is a Commentary on Sarkar *et al.*, 224: 886–901.

Trifold interactions have been transcriptomically analysed before (Lysøe *et al.*, 2017), but it is here, for the first time, that the transcriptomes of all partners were analysed together and in all bilateral combinations. This constitutes an important step forward in identifying and untangling direct from indirect effects of biocontrol on the level of transcriptional responses.

The first species among the order Sebaciales which has been analysed concerning its impact on plants during a nonmycorrhizal interaction was *Serendipita indica* (formerly *Piriformospora indica*). Isolated in 1998, it was first characterized as plant-growth promoting, later also as a biocontrol fungus, protecting plants against abiotic stresses and against soil-borne and leaf-invading pathogens (Franken, 2012). Alga Zuccaro and her group have made major contributions to the understanding of the biology of *S. indica* and its interaction with barley and Arabidopsis, including sequencing of its genome and transcriptomes (Zuccaro *et al.*, 2011), the role of phytohormones in the interaction (Lahrmann & Zuccaro, 2012), and the importance of nitrogen sensing by *S. indica* (Lahrmann *et al.*, 2013) and of proteins secreted by the fungus (Wawra *et al.*, 2019). First described as a *Rhizoctonia*-like fungus (Verma *et al.*, 1998), it turned out that *S. indica* belongs to an order of which members are associated with plant roots in mycorrhizal and nonmycorrhizal interactions (Selosse *et al.*, 2009). Of these, *Serendipita vermifera* (formerly *Sebacinia vermifera*) also showed beneficial effects on plants in nonmycorrhizal interactions (Barazani *et al.*, 2007; Ghimire & Craven, 2011).

The article by Sarkar *et al.* presents a ground-breaking study to investigate the bipartite and tripartite transcriptional responses in the interaction between *S. vermifera*, the root invading pathogen *B. sorokiniana* and barley. The elegant split-root system employed allowed dissection of local and systemic plant-mediated responses conveyed by the two fungi on each other. In addition, direct effects of the two fungal species, outside of the plant, were included.

Transcriptome analysis revealed that direct contact between both fungi resulted in induction of stress-related genes in the pathogen with concomitant repression of effector genes, and, in sharp contrast, genes for hydrolytic enzymes in the endophyte. The identification of the pathogen as the prey and the endophyte as the assailant in the interaction presents the first important finding of the article, especially as two parallel mechanisms are implied: impact on pathogen gene expression and enzymatic attack of the pathogen's cell wall. Remarkably, the plant host-induced changes in the fungal transcriptomes were not much affected by the co-colonizing fungus. It was only the absolute number of transcripts from the pathogen which was clearly reduced.

A collateral result, the article nicely shows the different strategies of the endophyte and the pathogen to live inside a plant root. Only a few transcriptional changes were observed in barley when inoculated solely with the endophytic strain and this confirms a previous assumption based on the analysis of only a few barley genes during

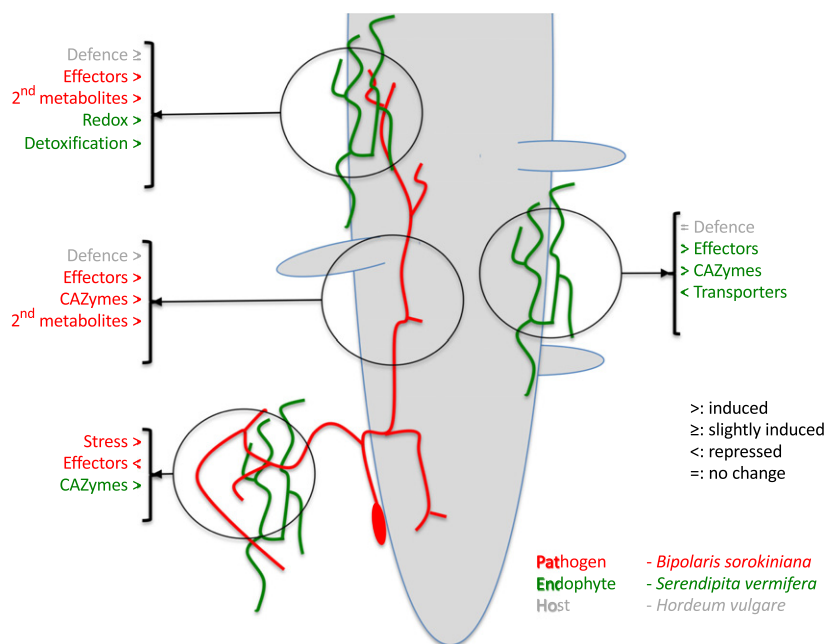


Fig. 1 Transcriptional changes during bipartite and tripartite interactions between *Serendipita vermifera*, *Bipolaris sorokiniana* and barley as described in this issue of *New Phytologist* by Sarkar *et al.* (pp. 886–901).

root colonization by *S. indica* (Waller *et al.*, 2008). This clear difference to a mycorrhizal interaction, where numerous plant genes are changed in their expression (Zhao *et al.*, 2019), is the second important finding. As expected, the presence of *B. sorokiniana* triggered changes in expression of numerous barley genes, the majority of the gene products being associated with plant immunity. This pattern of changes was the same in the tripartite interaction except for a quantitative effect concerning the number of pathogen-induced plant genes. This effect could be simply due to a decrease in both pathogen biomass and disease symptoms. It could, however, also be due to an impact of the endophyte on allocation of resources by influencing the gibberellin/jasmonate balance, as it was shown for *S. indica* in rice (Cosme *et al.*, 2016).

From these observations, it becomes clear that *S. vermifera* can directly affect gene expression in *B. sorokiniana*, and this possibly contributes to reduced pathogenicity in barley roots, for instance through reduced expression of effector genes. *Serendipita vermifera* shows a clear direct biocontrol effect already outside of the root, hence its designation as a ‘gatekeeper’. During root colonization, the expression of plant genes involved in defence responses were neither endophyte-enhanced (in the absence of the pathogen) nor endophyte-primed (in the presence of the pathogen). *Serendipita vermifera* biocontrol, therefore, seems not to be based on an indirect effect by inducing resistance. This is in sharp contrast to biocontrol by mycorrhizal fungi which induce defence genes already in the absence, but even more in the presence of root pathogens (Jung *et al.*, 2012). The situation is different in biocontrol of shoot pathogens. Here, it has been shown that colonization by sebacinoid endophytes and arbuscular mycorrhizal (AM) fungi both resemble the phenomenon of Induced Systemic Resistance (Pozo & Azcón-Aguilar, 2007; Stein *et al.*, 2008).

Our knowledge of the different types of root–fungus interactions is fragmentary. The literature is dominated by studies with AM

fungi, and some papers exist for pathogenic fungi and the sebacinoid endophyte *S. indica*. Debika Sarkar and colleagues applied a sophisticated experimental system for fungus–root–fungus interactions and accurately measured transcriptional reprogramming in all bipartite and tripartite combinations of three partners (Fig. 1). On the basis of the rich dataset, they clearly describe particular bilateral interaction types (antagonism, pathogenicity, endophytism) and their trifold interplay (biocontrol). Thereby, this study lets us catch a glimpse of the complexity of interactions in the rhizosphere.

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