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Epigenetic control is involved in molecular dialogue in plant-microbe symbiosis

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"… new insight concerning the effect of a modified epigenetic background of a host plant on its symbiotic relationship with a mycorrhizal fungal partner…"

Following the huge amount of insight in gene regulation at the transcriptional level by omic expression studies, revealing transcription factors and gene networks, a new step of whole genome regulation levels has added again more complexity to our understanding of gene expression control. Indeed, epigenetic processes affect also gene expression without changes in DNA sequences, as the chromatin structure is the molecular target of these mechanisms. In eukaryotes, the most common epigenetic modification is a DNA cytosine methylation that consists in the addition of a methyl group (CH_3) to a cytosine nucleotide. In plants, genomic DNA (gDNA) methylation is an extensively studied epigenetic mark that can occur in three sequence contexts, namely at the sites CG, CHG, and CHH (where H is A, T, C). Moreover, it is known that transposable elements (TEs) are presumed to be densely methylated and are thus inactive. Within last years, molecular mechanisms of DNA methylation have been extensively studied in model plants and recently reviewed (To & Kakutani, 2022; Kakoulidou & Johannes, 2023). Methodological knowhow for such analyses has been remarkably progressed using whole genome bisulfite sequencing (WGBS) performed on gDNA for full methylome analyses (Sow *et al*., 2021). Moreover, machine learning for systematic detection of differentially methylated regions (DMRs) was developed and reported recently (Hüther *et al*., 2022). However, few data are so far known regarding the link of epigenetics and plant-microbe interactions (Satgé *et al*., 2016; Ramos-Cruz *et al*., 2021). Regarding the formation of root nodules as new organs within the legume–Rhizobium symbiosis, Satgé *et al*. (2016) identified DNA methylation to play a determining role in *Medicago truncatula* nodules. A demethylase gene, called DEMETER (DME), is involved in the regulation of a high number of genes implicated in plant and bacterial cell differentiation required for nodule organogenesis in symbiotic interactions. Later, Ramos-Cruz et al. (2021) have stated that in addition to host genotypes and the environment, also the host epigenotype will determine the outcome of biotic interactions, potentially leading to plant defense, symbiosis or parasitism. In the case of arbuscular mycorrhizal (AM) symbiosis, first studies have shown that epigenetic modifications occur in seeds of *Geranium sylvaticum* or in roots and leaves of *Geranium robertianum* in symbiosis with the AM fungus *Funneliformis mosseae* (Varga & Soulsbury, 2017, 2019). In this issue of *New*

Phytologist, Vigneaud *et al*. (pp. 000-000) analyzed gene regulation at the epigenetic level interfering with ectomycorrhizal (ECM) interaction.

Here, the Authors gathered new insight concerning the effect of a modified epigenetic background of a host plant on its symbiotic relationship with a mycorrhizal fungal partner.

Vigneaud *et al*. (2023) took the symbiotic model plant poplar (*Populus tremula* x *Populus alba*) and its ECM fungus *Laccaria bicolor* and used previously produced six independent epigenetic-modified plant lines obtained by overexpression or RNAi. These transgenic poplar lines were two overexpressing-lines for the demethylases Demeter-Like *DML* (*OX-dml1* and *OX_dml2*) and two RNAi lines for the chromatin remodeler *DDM1* (Decreased in DNA Methylation 1). DDM1, conserved in animals, yeast, and plants, is known to facilitate methylation by providing access for DNA methyltransferase. A strong decrease of *DDM1* expression levels in the model plant *Arabidopsis thaliana* resulted in a significant reduction of DNA methylation (Lippman *et al*., 2004). All these four poplar lines are hypomethylated lines. The two other used poplar mutants were RNAi-mediated hypermethylated *DML* lines (Sow *et al*., 2021). The level of DNA methylation of the host tree being manipulated in these transgenic plant lines, the authors observed differential gene and TE methylation together with differential gene expression, linked to reduced mycorrhization rates only for the hypomethylated lines. Comparison of wild-type poplar with poplar lines with modified DNA methylation levels showed not only differentially methylated plant genes (86) and TEs (288) and, remarkably, differentially methylated fungal genes (120) and TEs (1441), but also that such manipulation will affect in turn mycorrhizal interactions. In fact, the fungus methylome will become altered when the colonizing fungus interacts with poplar hosts with hypomethylated gDNA, suggesting that disturbing the control of poplar methylation will induce also the remodeling of the fungal genomic methylome. Moreover, hypomethylated poplar results in differential gene (205) expression. From these results, the authors suggested poplar gene candidates potentially involved in physiological processes that could be linked to mycorrhizal interaction, as root initiation, immune responses, hormonal pathways (ethylene and jasmonate), or terpenoid metabolism. Such candidates will need further analyses to rule out their specific roles and regulation.

The study by Vigneaud *et al*. (2023) concludes that a number of host genes under epigenetic control is involved in the mutualistic interaction highlighting a new level of gene regulation to the rather complex interaction between host plants and microbial symbionts. In the context of ECM symbiosis playing a major role for nutrition, health and stress tolerance of host trees, these new findings increase our knowledge about the tightly regulated crosstalk between symbiotic partners.

Interestingly, the impact of DNA methylation for plant genomic immunity has been demonstrated (Kim & Zilberman, 2014; Hannan Parker *et al*., 2022; Huang & Jin, 2022). Plants have evolved sophisticated and tightly regulated methylation and demethylation pathways to protect their genes against damage by transposon invasions (Kim & Zilberman, 2014). In response to biotic stress, epigenetic regulation, including DNA methylation, histone and chromatin structure modifications, has been reported to be involved in plant immunity against interacting pathogens (Huang & Jin, 2022). As plants as sessile organisms without specialized cells for immune responses need to tolerate and resist a number of abiotic and biotic stress conditions, among them pathogen attacks, these epigenetic regulation tools are of high importance for survival and adaptation. Moreover, epigenetic modifications can be heritable and thus contribute to the defense priming and transgenerational memory. In fact, biotic stress will alter DNA methylation and modification of the epigenetic regulation would affect resistance to plant diseases (Hannan Parker *et al*., 2022). Research findings in this field have clearly demonstrated a link between plant immunity and TE hypomethylation (Wilkinson *et al*., 2019).

As beneficial plant-microbe interactions occur at a border of plant defense and establishment of symbiotic relations, it could be expected that a tight epigenetic control between host and symbiont would also be involved and needed in this process. Moreover, comparison between beneficial symbiotic interactions and pathogenic attacks might give further clues on the specific impact of epigenetic control between "friend and foe". In perspective, a comparison of epigenetically regulated plant genes as reported in the context of drought stress (Sow *et al*., 2021) without and with the fungal ectomycorrhizal partner in the wild-type situation would be interesting to advance the knowledge on the reciprocal crosstalk between both symbiotic partners. In addition, an interesting open question is whether epigenetic regulatory mechanisms might be involved in induced systemic resistance (ISR) by beneficial microbes (Pieterse *et al*., 2014).

Altogether, Vigneaud *et al*. (2023) convincingly and nicely demonstrated with their contribution the impact of the host plant epigenetic machinery on the interaction with a beneficial ectomycorrhizal fungus. A series of further challenging questions concerning the crosstalk between host plant and beneficial microbes, the specificity of beneficial interactions compared to pathogen attacks, and the involvement of epigenetic regulation in reported ISR might be raised in future research. Finally, more generally, these questions will become important to master plant-microbe interactions, priming of defense and/or better use of beneficial associations.

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