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

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21 Following the huge amount of insight in gene regulation at the transcriptional level
22 by omic expression studies, revealing transcription factors and gene networks, a
23 new step of whole genome regulation levels has added again more complexity to
24 our understanding of gene expression control. Indeed, epigenetic processes affect
25 also gene expression without changes in DNA sequences, as the chromatin
26 structure is the molecular target of these mechanisms. In eukaryotes, the most
27 common epigenetic modification is a DNA cytosine methylation that consists in the
28 addition of a methyl group (CH₃) to a cytosine nucleotide. In plants, genomic DNA
29 (gDNA) methylation is an extensively studied epigenetic mark that can occur in
30 three sequence contexts, namely at the sites CG, CHG, and CHH (where H is A, T,
31 C). Moreover, it is known that transposable elements (TEs) are presumed to be
32 densely methylated and are thus inactive. Within last years, molecular
33 mechanisms of DNA methylation have been extensively studied in model plants
34 and recently reviewed (To & Kakutani, 2022; Kakoulidou & Johannes, 2023).
35 Methodological knowhow for such analyses has been remarkably progressed using
36 whole genome bisulfite sequencing (WGBS) performed on gDNA for full methylome
37 analyses (Sow *et al.*, 2021). Moreover, machine learning for systematic detection
38 of differentially methylated regions (DMRs) was developed and reported recently
39 (Hüther *et al.*, 2022). However, few data are so far known regarding the link of
40 epigenetics and plant-microbe interactions (Satgé *et al.*, 2016; Ramos-Cruz *et al.*,
41 2021). Regarding the formation of root nodules as new organs within the legume-
42 *Rhizobium* symbiosis, Satgé *et al.* (2016) identified DNA methylation to play a
43 determining role in *Medicago truncatula* nodules. A demethylase gene, called
44 DEMETER (DME), is involved in the regulation of a high number of genes implicated
45 in plant and bacterial cell differentiation required for nodule organogenesis in
46 symbiotic interactions. Later, Ramos-Cruz *et al.* (2021) have stated that in addition
47 to host genotypes and the environment, also the host epigenotype will determine
48 the outcome of biotic interactions, potentially leading to plant defense, symbiosis
49 or parasitism. In the case of arbuscular mycorrhizal (AM) symbiosis, first studies
50 have shown that epigenetic modifications occur in seeds of *Geranium sylvaticum*
51 or in roots and leaves of *Geranium robertianum* in symbiosis with the AM fungus
52 *Funneliformis mosseae* (Varga & Soulsbury, 2017, 2019). In this issue of *New*

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

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

58 Vigneaud *et al.* (2023) took the symbiotic model plant poplar (*Populus*
59 *tremula* x *Populus alba*) and its ECM fungus *Laccaria bicolor* and used previously
60 produced six independent epigenetic-modified plant lines obtained by
61 overexpression or RNAi. These transgenic poplar lines were two overexpressing-
62 lines for the demethylases Demeter-Like *DML* (*OX-dml1* and *OX_dml2*) and two
63 RNAi lines for the chromatin remodeler *DDM1* (Decreased in DNA Methylation 1).
64 *DDM1*, conserved in animals, yeast, and plants, is known to facilitate methylation
65 by providing access for DNA methyltransferase. A strong decrease of *DDM1*
66 expression levels in the model plant *Arabidopsis thaliana* resulted in a significant
67 reduction of DNA methylation (Lippman *et al.*, 2004). All these four poplar lines
68 are hypomethylated lines. The two other used poplar mutants were RNAi-mediated
69 hypermethylated *DML* lines (Sow *et al.*, 2021). The level of DNA methylation of
70 the host tree being manipulated in these transgenic plant lines, the authors
71 observed differential gene and TE methylation together with differential gene
72 expression, linked to reduced mycorrhization rates only for the hypomethylated
73 lines. Comparison of wild-type poplar with poplar lines with modified DNA
74 methylation levels showed not only differentially methylated plant genes (86) and
75 TEs (288) and, remarkably, differentially methylated fungal genes (120) and TEs
76 (1441), but also that such manipulation will affect in turn mycorrhizal interactions.
77 In fact, the fungus methylome will become altered when the colonizing fungus
78 interacts with poplar hosts with hypomethylated gDNA, suggesting that disturbing
79 the control of poplar methylation will induce also the remodeling of the fungal
80 genomic methylome. Moreover, hypomethylated poplar results in differential gene
81 (205) expression. From these results, the authors suggested poplar gene
82 candidates potentially involved in physiological processes that could be linked to
83 mycorrhizal interaction, as root initiation, immune responses, hormonal pathways
84 (ethylene and jasmonate), or terpenoid metabolism. Such candidates will need
85 further analyses to rule out their specific roles and regulation.

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

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

109 As beneficial plant-microbe interactions occur at a border of plant defense
110 and establishment of symbiotic relations, it could be expected that a tight
111 epigenetic control between host and symbiont would also be involved and needed
112 in this process. Moreover, comparison between beneficial symbiotic interactions
113 and pathogenic attacks might give further clues on the specific impact of epigenetic
114 control between "friend and foe". In perspective, a comparison of epigenetically
115 regulated plant genes as reported in the context of drought stress (Sow *et al.*,
116 2021) without and with the fungal ectomycorrhizal partner in the wild-type
117 situation would be interesting to advance the knowledge on the reciprocal crosstalk
118 between both symbiotic partners. In addition, an interesting open question is

119 whether epigenetic regulatory mechanisms might be involved in induced systemic
120 resistance (ISR) by beneficial microbes (Pieterse *et al.*, 2014).

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

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188 **Key words**

189 ectomycorrhizal fungus, epigenetic control, host tree, hypomethylation, *Laccaria*
190 *bicolor*, mycorrhizal symbiosis, poplar, transposable element