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► **To cite this version:**

Noureddine Lazar, Yohann Petit-Houdenot, Nacera Talbi, Inès Li de la Sierra-Gallay, Zélie Emilie, et al.. Two avirulence genes of *Leptosphaeria maculans*, displaying suppressive interactions, share a common structural pattern and are part of a larger effector family. Effectome meeting, Oct 2019, Lauret, France. hal-04456391

HAL Id: hal-04456391

<https://hal.science/hal-04456391v1>

Submitted on 13 Feb 2024

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Two avirulence genes of *Leptosphaeria maculans*, displaying suppressive interactions, share a common structural pattern and are part of a larger effector family

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Recognition of a pathogen avirulence (AVR) protein triggers a set of immune responses grouped under the term Effector-Triggered Immunity (ETI). Pathogens can escape ETI by different mechanisms including complete deletion or down-regulation of the AVR genes, point mutations allowing recognition to be evaded while maintaining the virulence function of the AVR protein, and acquisition of new effectors able to suppress recognition. In some cases, the effector that suppresses ETI can itself be recognized by an R gene. A few examples of such mechanism were recently described in fungi but the underlying mechanisms have remained unexplained.

The Dothideomycete *Leptosphaeria maculans*, causal agent of oilseed rape stem canker, is one of the fungal pathogens in which suppression of ETI by the presence of an AVR gene has been demonstrated. The AVR gene *AvrLm4-7* was reported to hide *AvrLm3* from *Rlm3*-mediated recognition and *AvrLm5-9* from *Rlm9*-mediated recognition (Plissonneau et al., 2016; Ghanbarnia et al., 2018). The way *AvrLm4-7* suppresses recognition of *AvrLm3* and *AvrLm5-9* by their cognate R genes is not known: the presence of *AvrLm4-7* does not impede *AvrLm3* and *AvrLm5-9* expression and yeast two-hybrid assays suggested the absence of a physical interaction between *AvrLm4-7*, *AvrLm5-9* and *AvrLm3*. While *AvrLm5-9* and *AvrLm3* share a low level of identity, no homology was found with *AvrLm4-7*.

Blondeau et al. (2015) previously determined the crystal structure of *AvrLm4-7*. We recently determined of the crystal structure of *AvrLm5-9*. Surprisingly, despite a lack of sequence similarity, *AvrLm5-9* shares structural analogies with *AvrLm4-7* (a four stranded anti-parallel sheet and two disulfide bridges in common). This suggests that the antagonistic interaction between *AvrLm5-9* and *AvrLm4-7* could be due to a competition for a same plant target. Structure-informed and pattern-based searches identified a larger number of structural analogues among *L. maculans* effector candidates (including *AvrLm3*) and a limited number of structural analogues in other phytopathogenic fungi (including ECP11-1 from *Passalora fulva*, which shares homologies with *AvrLm3*; Mesarich et al., 2018). We determined the crystal structure of ECP11-1 and confirmed it shared structural analogies with *AvrLm4-7* and *AvrLm5-9*. Transformants of *L. maculans* expressing *ECP11-1* triggered *Rlm3*-mediated recognition, and that recognition was suppressed by *AvrLm4-7*, suggesting either that ECP11-1 has the same function as *AvrLm3*, or that its structure is sufficiently close to that of *AvrLm3* to be recognized by *Rlm3*.