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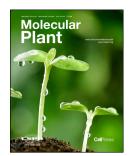
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RNA Splicing: A Novel Pathogen Effector Target

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Potato late blight caused by the notorious oomycete pathogen *Phytophthora infestans* led to the Irish famine in the middle 1840s. This disease still remains a challenge for potato production. Effector proteins help *P. infestans* to infect their host plants including potato and tomato. In summer 2004, in Joint Genome Institute (JGI, Walnut Creek, California), some *Phytophthora* researchers gathered at an "Effector table", and by aligning the amino acid sequences of many unpublished effector proteins from *Phytophthora* pathogens, revealed that all of them possess conserved Arg-any residue-Leu-Arg (RXLR) and Glu-Glu-Arg (EER) motifs post signal peptides (Govers, 2006). In 2009, the genome sequence of *P. infestans* strain T30-4 was published and 563 RXLR effectors were predicted. Since then, many high-throughput "effectoromics" screening strategies have been developed and some new effectors have been identified that trigger a hypersensitive response (HR), or that function as cell death repressors or RNA silencing suppressors. However, the function of most RXLR effectors still remains unknown.

A new study by Huang et al. (2020) discovered that *Phytophthora* effectors can reprogram host immunity through moldulating alternative splicing (AS) of host mRNAs in tomato. Plant immune systems operate in multiple layers, one of which involves AS that is known to play roles in both microbe-associated molecular pattern (MAMP)-triggered immunity and effector-triggered immunity. To gain insight into potential AS-regulated plant immunity during pathogen attack, Huang et al. (2020) firstly investigated tomato transcriptome changes during *P. infestans* infection and identified 2,088 alternatively spliced genes in response to pathogen infection. To investigate how *P. infestans* manipulates plant AS and to identify specific splicing regulatory effectors (SREs), they developed an alternative splicing reporter system, in which the alternatively spliced region of *RLPK*, a known protein kinase gene that undergoes AS upon pathogen attack, is fused with the *luciferase* (LUC) gene and a stable *35S-RLPK-LUC* transgenic *Nicotiana benthamiana* line was generated. The *RLPK.1* transcript produces functional luciferase, but upon alternative splicing, the *RLPK.2* carries a premature stop codon, preventing luciferase expression. Using this system, they tested 87

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RXLR effectors from *P. infestans* and identified 9 SREs. Furthermore, they found these SREs bind splicing factors to modulate plant AS. Specifically, SRE3 (Pi06094) can physically interact with a splicing factor U1-70k and promote virulence of *P. infestans* (Huang et al., 2020).

The versatile reporter system for identifying AS-regulating effectors developed by Huang et al. (2020) could be applied to other plant pathogens and will deepen our understanding of how alternative splicing manipulates plant immunity. It is noteworthy that one of the SREs (SRE4, PITG_07569) was recently reported as the Avr effector of a broad-spectrum R gene Rpi-amr1 from Solanum americanum (Lin et al., 2020). Investigating how these SREs interact with their host targets to modulate AS and how plant immune receptors can recognize them to activate host immunity might lead to new disease control strategies.



Figure 1. Potato field with late blight infection.

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