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A Decade Decoded: Spies and Hackers in the History of TAL Effectors Research

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Abstract

The *Xanthomonas* genus produces proteins called transcription activator-like effectors (TALEs), which have the extraordinary capacity to directly bind gene promoters in plant hosts and increase their expression, hence aiding in bacterial colonization. In a metaphorical sense, TALEs enter the plant like spies camouflaged as senior citizens (transcription factors) in order to deceive the plant into turning on vulnerabilities that permit an invasion. Because of our current understanding of TALE behavior, researchers are able to anticipate their actions (counterespionage) and take use of their capabilities, manipulating them to serve as Manchurian agents. This has been made feasible in part by the identification of their DNA binding mechanism, which complies with the TALE code, a set of specific amino acid–DNA correspondences.

Introduction

When it comes to the "evolutionary escalation of ever more defined mutual counter-adaptations" in antagonistic interactions between species, the idea of an arms race is a ubiquitous parallel from combat, In plant pathology, this idea is utilized to emphasize the genetic and biochemical coevolutionary patterns that have developed between diseases and their plant hosts. In According to the zigzag model, the molecular plant-pathogen arms race may be explained as a sequence of attacks carried out by effectors that enhance the pathogen's virulence and counterattacks carried out by defenses that are deployed when the pathogen is identified. Effectors can be employed to weaken a plant's defenses, but they can also give a pathogen a place to live by letting it take advantage of the resources in the plant.

PART I: NI-NG-NI-HD-NI-NS (1880s–2009)

The Yellow Forms: Early Developments in Plant Bacteriology

Various Xanthomonas species were among the first described plant bacterial pathogens and their name was defined in 1939 to classify "the yellow forms with a single polar flagellum". It is a genus that now includes ~27 worldwide-spread bacterial species causing diseases on more than 120 monocotyledonous and 260 dicotyledonous species. Several other diseases were described in the early twentieth century, and their description was accompanied with attempts (Bogdanove *et al.*, 2010) to look for a mechanistic understanding of the interactions. Plant pathologists were early adopters of Mendel's genetic principles, and since 1905 resistance to pathogens was identified as an inheritable, often monogenic, trait. In 1946, a proposal stated that "for each factor for resistance in the host there was a specific factor for virulence in the pathogen".

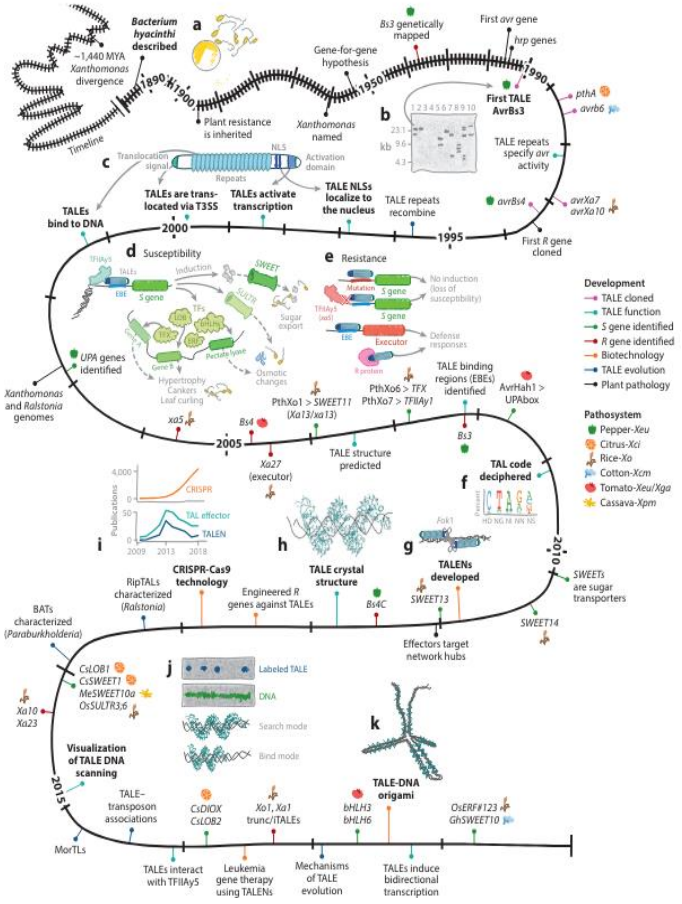

Fig 1- Timeline of transcription activator–like effector (TALE) research (Perez-Quintero and Szurek., 2019)

Two Decades of Uncovering TALE Functions

Since bacterial hrp genes were required for the avrBs3-mediated HR response in planta and were already thought to be involved in the production of a protein secretion system (type III), it was assumed that the bacteria secreted and translocated TALEs (45, 69). Eventually, it was discovered that the N-terminal portion of TALEs had a translocation signal area, which was necessary for their secretion through the type III secretion system (T3SS). Conversely, it was discovered that all known members of the AvrBs3/PthA family have putative motifs in their C-terminal regions that resembled monopartite nuclear localization signals (NLSs) (142). When the NLSs were fused to GUS (β-glucuronidase) reporter proteins (Moscou and Bogdanove., 2009).

PART II: NN-NI-NG-NG-NI-HD-HD-NI (2009–2019)

The Remarkably Beautiful Structure of TALEs

The next big mystery in TALE research was: How exactly did the protein interact with DNA? Early in silico analyses predicted each repeat unit to form two α-helices, whereas the whole protein was proposed to generate a right-handed α-α-helical superstructure, with possibly two intertwined helices corresponding to TALE homodimers that had been shown to form in planta. In 2012, two groups reported for the first time two crystal structures of the full repeat region of TALEs: The X. oryzae TALE PthXo1 bound to its target DNA, and the structure of a designer TALE (dHax3, made to mimic Hax3 from Xca) bound to a target DNA and in its free form. Since then, several other crystal structures of TALEs have been published, including those of PthA, AvrBs3, a TALE-like protein from *Paraburkholderia rhizoxinica*, and various engineered TALEs binding to custom DNA sequences, RNA–DNA hybrids, and methylated DNA (Perez-Quintero and Szurek, 2019).

TALE Applications in Biotechnology:

Cassette Tapes or Vinyl Records

TALEs' biotechnological applications have been envisioned since the publication of the code, when the first designer or artificial TALE was created. Designer TALEs were soon shown to be functional in various eukaryotic systems, and they offer the possibility of targeting any promoter sequence in a genome for their transcriptional induction. However, the main success of TALEs in biotechnology stemmed from the ability to fuse their DNA binding domain to several other functional domains for site-directed DNA manipulation. One of the most notorious of such applications is the use of TALE nuclease

Plants resistance against TALEs

The two forms of dominant R genes that plants can use to counterattack are TALE-dependent (executor) and non-transcriptional (classical) genes. Genes that detect the TALE through interactions between proteins are known as classical R genes. Three of these gene types have so far been identified: Leucine-rich TIR-NBS-LRR (Toll-interleukin 1-nucleotide binding site) is encoded by Bs4 and Xa1. return) from tomato and an NBS-LRR from rice, in that order; also, Xo1 from non-cloned rice. In all three instances, 3.5 repetitions appeared to be adequate for identification, and they have all been demonstrated to initiate resistance in response to TALEs in a way independent of their transcriptional activity. Despite the lack of evidence for a direct connection, recognition has been suggested to take place in the cytoplasm (Schreiber *et al.*, 2019).

TALEs target and their role in defense

The introduction of multiple members of the SWEET (generically derived from "sugars will eventually be exported transporters") (also known as MtN3/saliva/Nodulin-3) family of sugar transporters by TALEs from diverse pathovars and species is one of the most well-researched instances of target convergence in TALEs. These proteins serve as sugar uniporters, facilitating the import and sugar efflux in plant and animal cells. This family contains significant S genes for Xoo in rice; at least three members of the family are targeted by various strains, and in certain situations (like SWEET14), multiple TALEs target the same gene at various binding sites. Members of the SWEET family are likewise TALE targets for Xcm.

Conclusion

By stealthily entering the plant nucleus and deceiving the host into activating susceptibility genes that permit bacterial colonization, TALEs operate like spies. Repeat sections found in TALEs bind plant

DNA according to particular correspondences between nucleotides and amino acids (TALE code). The identification of the TALE code facilitated the development of novel biotechnologies as well as the prediction and validation of new roles in interactions between plants and bacteria. TALEs have distinct DNA binding methods and a distinct structure. Xanthomonas has a variety of TALEs that quickly evolve to fit into different hosts.

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