



Available online at www.sciencedirect.com

ScienceDirect



REVIEW

Action modes of transcription activator-like effectors (TALEs) of *Xanthomonas* in plants



XU Zheng-yin, ZOU Li-fang, MA Wen-xiu, CAI Lu-lu, YANG Yang-yang, CHEN Gong-you

School of Agriculture and Biology/State Key Laboratory of Microbial Metabolism, Shanghai Jiao Tong University, Shanghai 200240, P.R.China

Abstract

Plant-pathogenic *Xanthomonas* infects a wide variety of host plants and causes many devastating diseases on crops. Transcription activator-like effectors (TALEs) are delivered by a type III secretion system (T3SS) of *Xanthomonas* into plant nuclei to directly bind specific DNA sequences (TAL effector-binding elements, EBEs) on either strand of host target genes with an unique modular DNA-binding domain and to bidirectionally drive host gene transcription. The target genes in plants consist of host susceptibility (*S*) genes promoting disease (ETS) and resistance (*R*) genes triggering defense (ETI). Here we generally summarized the discovery of TALEs in *Xanthomonas* species, their functions in bacterial pathogenicity in plants and their target genes in different host plants, and then focused on the newly revealed modes of protein action in triggering or suppressing plant defense.

Keywords: *Xanthomonas*, TALE, iTALE, ETS, ETI, suppressor

1. Introduction

Xanthomonas, a genus of γ -subdivision of the Proteobacteria, consists of a diverse group of Gram-negative bacterial plant pathogens that collectively infect a wide variety of host plants, including 124 monocotyledonous and 268 dicotyledonous plant species (Hayward *et al.* 1993). Despite the wide host range of *Xanthomonas*, each individual strain can be highly restricted to particular plants, generally from

the same botanical family (Jacques *et al.* 2016). According to the relatively narrow host range and tissue specificity, individual *Xanthomonas* strains are grouped into different pathovars (pv.) that were defined as an infra-subspecific group of strains causing the same disease on the same host range, such as *X. oryzae* pv. *oryzae* (*Xoo*) and *X. oryzae* pv. *oryzicola* (*Xoc*) (Dye *et al.* 1980). Different *Xanthomonas* pathovars can colonize at almost all organs (i.e., stems, twigs, leaves, flowers, buds, fruits, seeds and roots) of a plant and gain access to the tissues through natural openings (i.e., stomata, hydathodes, lenticels, and nectaries) and wounds (Jacques *et al.* 2016). Symptoms caused by the bacteria comprise leaf spots, leaf streaks, stripes, wilt, necrosis, blights, cankers and gummosis on leaves, fruits or stems (Hayward *et al.* 1993; Jacques *et al.* 2016).

Many devastating diseases are caused by members of *Xanthomonas*, which lead to severe impact on yield quantity and quality of economically important crops such as rice,

Received 13 April, 2017 Accepted 30 August, 2017
XU Zheng-yin, E-mail: xuzy2015@sjtu.edu.cn; Correspondence
CHEN Gong-you, Tel: +86-21-34205873, E-mail: gyouchen@sjtu.edu.cn

© 2017, CAAS. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>)
doi: 10.1016/S2095-3119(17)61750-7

wheat, cotton, bean, citrus, pepper, tomato, mango, and cabbage (Schornack et al. 2013). For example, bacterial blight (BB) and bacterial leaf streak (BLS) of rice (*Oryza sativa*) are caused by the vascular pathovar *Xoo* and the non-vascular pathovar *Xoc*, respectively (Niño-Liu et al. 2006). Both diseases constrain production of rice crop in much of Asia and parts of Africa and Australia (Schornack et al. 2013). BB was one of the most destructive diseases of rice-growing regions worldwide and its damage was reported to range from 10 to 100% (Mew et al. 1993; Schornack et al. 2013). In addition to reducing yield, BB may also affect grain quality by interfering with maturation (Niño-Liu et al. 2006). BLS has typically caused less damage in rice and yield losses range from 5 to 30% depending on the rice variety and climatic conditions, but it is more devastating than BB in China (Zou et al. 2011; Schornack et al. 2013; Ji et al. 2014).

Not all, but many disease-causing *Xanthomonas* species deploy proteins called transcription activator-like effectors (TALEs) to infect their host plants (Boch and Bonas 2010; Jacques et al. 2016). TALE proteins are injected into plant cells via a type III secretion system (T3SS), and then they enter the nucleus and modulate expression of host genes (Bogdanove et al. 2010; Scholze and Boch 2011). Numerous breakthroughs in the field of TALE biology have been made since the discovery of the first TALE, which has improved our understanding of bacterial disease processes. This review covers most recent advances with a focus on the action modes of TALEs in plants.

2. Discovery of TALEs

The AvrBs3 protein from the pepper and tomato pathogen *X. campestris* pv. *vesicatoria* (*Xcv*) was the first member of TALEs identified (Bonas et al. 1989). Shortly after that, several members of TALEs were reported in a variety of *Xanthomonas* species, including PthA from *X. citri* (Swarup et al. 1991, 1992; Duan et al. 1999), Avrxa5, AvrXa7 and AvrXa10 from *X. oryzae* pv. *oryzae* (Hopkins et al. 1992; Bai et al. 2000), Avrb6, Avrb4, Avrb7, AvrbIn, Avrb101, Avrb102, Avrb103, Avrb104 and Avrb5 from *X. campestris* pv. *malvacearum* (Gabriel et al. 1986; De Feyter et al. 1993; Yang et al. 1996). Revealing the mechanism of TALE function in plant is time consumption in efforts. The first clue came from the observation of functional nuclear localization signals (NLSs) in the C-terminus of AvrBs3, which was shown by fusion proteins transiently expressed in onion and genetic studies (Yang and Gabriel 1995; Van den Ackerveken et al. 1996). Moreover, an acidic activation domain (AD) was also found at the C-termini of TALEs (Zhu et al. 1998, 1999; Szurek et al. 2001). The presence of two typical eukaryotic motifs, NLS and AD, suggested a nuclear targeting activity of the protein family in plant

cells (Van den Ackerveken et al. 1996; Szurek et al. 2001; Marois et al. 2002). Subsequent studies demonstrated that TALEs indeed localize to the plant cell nucleus by T3SS-dependent delivery (Yang et al. 2000; Szurek et al. 2002; Büttner et al. 2004). In addition, TALEs dimerize in the plant cell cytoplasm prior to nuclear import (Gürlebeck et al. 2005). The discovery of the DNA binding and gene expression induction activity of the TALEs (Kay et al. 2007, 2009; Römer et al. 2007, 2009b), together with the fact that nuclear targeting is essential for function, gives the moniker “transcription activator-like (TAL)” to the protein family (Mak et al. 2013). TALEs differ in the middle, a repetitive 33–35 amino acids long region, which determine the specificity of DNA binding (Kay et al. 2009). A hallmark pair of reports both experimentally and computationally elucidated the code involved in the protein-DNA recognition (Boch et al. 2009; Moscou and Bogdanove 2009). The structures of TALEs and TALE-DNA complex were solved in early 2012, which provided a clear view of the structural basis for the DNA recognition code (Deng and Yan 2012; Mak et al. 2012).

3. The number and virulence function of TALEs

According to a survey for available genome sequences and literature, TALE-encoding (*tal*) genes have been found in at least 12 *Xanthomonas* species, including *X. alfalfae*, *X. euvesicatoria*, *X. citri*, *X. axonopodis*, *X. oryzae*, *X. campestris*, *X. hortorum*, *X. gardneri*, *X. cassavae*, *X. theicola*, *X. hyacinthi*, *X. translucens* and so on (Jacques et al. 2016). Different *Xanthomonas* pathovars and strains have evolved varying numbers of TALEs (Schornack et al. 2013). Some pathovars carry none or only few *tal* genes, such as *X. campestris* pv. *campestris*, *X. citri*, *X. axonopodis* pv. *glycines* and *X. translucens* pv. *translucens* (Da Silva et al. 2002; Al-Saadi et al. 2007; Park et al. 2008; Schornack et al. 2013; Ye et al. 2013). However, others contain a fair amount of *tal* genes, such as pathovars of *X. oryzae*. More than 8 *tal* genes in different genomes of *Xoo* strains have been characterized (Lee et al. 2005; Ochiai et al. 2005; Gonzalez et al. 2007; Salzberg et al. 2008; Yu et al. 2011), while much richer *tal* genes, up to 28, are harbored in some *Xoc* strains (Bogdanove et al. 2011; Ji et al. 2014; Booher et al. 2015).

Although the activity of TALEs as transcriptional activators and their DNA-binding code is clear, our understanding of their role in bacterial virulence is still restricted to a few of them. The first example was PthA from *X. citri*, which causes citrus canker, hyperplasia, and hypertrophy, potentially allowing better dissemination of apoplasmic bacteria (Swarup et al. 1991; Yang et al. 1994). Avrb6 from *X. campestris* pv. *malvacearum* is

Download English Version:

<https://daneshyari.com/en/article/8875763>

Download Persian Version:

<https://daneshyari.com/article/8875763>

[Daneshyari.com](https://daneshyari.com)