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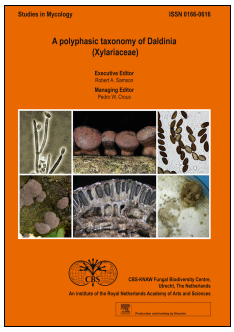

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Two different *R* gene loci co-evolved with *Avr2* of *Phytophthora infestans* and confer distinct resistance specificities in potato

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Key words: *Avr* gene, co-evolution, resistance, late blight, *Phytophthora infestans*, potato, *R* gene, *Solanum*.

Abstract: Late blight caused by the oomycete pathogen *Phytophthora infestans* is the most devastating disease in potato. For sustainable management of this economically important disease, resistance breeding relies on the availability of resistance (*R)* genes. Such *R* genes against *P. infestans* have evolved in wild tuber-bearing *Solanum* species from North, Central and South America, upon co-evolution with cognate avirulence (*Avr*) genes. Here, we report how effectoromics screens with *Avr2* of *P. infestans* revealed defence responses in diverse *Solanum* species that are native to Mexico and Peru. We found that the response to AVR2 in the Mexican *Solanum* species is mediated by *R* genes of the *R2* family that resides on a major late blight locus on chromosome IV. In contrast, the response to AVR2 in Peruvian *Solanum* species is mediated by *Rpi-mcq1*, which resides on chromosome IX and does not belong to the *R2* family. The data indicate that AVR2 recognition has evolved independently on two genetic loci in Mexican and Peruvian *Solanum* species, respectively. Detached leaf tests on potato cultivar Désirée transformed with *R* genes from either the *R2* or the *Rpi-mcq1* locus revealed an overlapping, but distinct resistance profile to a panel of 18 diverse *P. infestans* isolates. The achieved insights in the molecular *R - Avr* gene interaction can lead to more educated exploitation of *R* genes and maximize the potential of generating more broad-spectrum, and potentially more durable control of the late blight disease in potato.

INTRODUCTION

Potato (*Solanum tuberosum* L) is the most important non-cereal crop consumed worldwide and is affected by the destructive late blight disease. The oomycete pathogen *Phytophthora infestans* is the causal agent of the disease, which destroys leaves, stems and tubers from growing potato plants (Fry 2008). In Ireland, late blight destroyed a large portion of the crop and led to the Irish potato famine between 1845 and 1849, causing the death of over one million people and the emigration of one million more (Zadoks 2008). Currently, late blight is the major threat to potato production, responsible for yield losses of around 16 % of the global crop and representing an annual financial loss of approximately € 6 billion (Haverkort *et al.* 2016).

Johanna Westerdijk believed that studying mechanisms that underlie plant immunity would help the breeding of resistant genotypes. In her inaugural lecture in 1917, when she became Professor of Phytopathology at Utrecht University, she described that diseases were most severe when pathogens or hosts are introduced in novel environments. She argued that co-evolution of hosts and pathogens is required for the evolution of resistance (Westerdijk 1917). In the meantime, significant progress has been made in understanding plant immunity, and this knowledge has led to the development of resistant plants. Several *R* genes conferring **R**esistance to ***P****hytophthora* ***i****nfestans* (*Rpi*) have been introgressed into potato cultivars from *Solanum* species native to Mexico (Malcolmson & Black 1966). The Toluca Valley in Mexico is a center of diversity for *P. infestans* and suggested to be the center of origin (Goodwin *et al.* 1992, Fry *et al.* 1993, Grunwald & Flier 2005). The Mexican resistance (*R)* genes include *R1-R11* from *Solanum demissum*, *Rpi-blb1, Rpi-blb2* and *Rpi-blb3* from *Solanum bulbocastanum, Rpi-sto1* and *Rpi-pta* from *Solanum stoloniferum* and *Rpi-amr3* from *Solanum americanum* (Hein *et al.* 2009, de Vetten *et al.* 2011, Vleeshouwers *et al.* 2011b, Jo *et al.* 2015, Witek *et al.* 2016). Some of these Mexican *R* genes belong to large gene families, such as *R2* that occurs at a major late blight resistance locus (MLB) on chromosome IV (Park *et al.* 2005a, Lokossou *et al.* 2009). In the Andean region in South America, the other center of genetic diversity of tuber-bearing *Solanum* (Hijmans & Spooner 2001, Spooner *et al*. 2004) as well as *P. infestans* (Abad & Abad 1997, Alpizar-Gomez *et al.* 2007), additional *R* genes have been identified. These include *Rpi-mcq1*, *Rpi-vnt1*, *Rpi-ber, Rpi-chc1, Rpi-tar1 from Solanum mochiquense, Solanum venturii*, *Solanum berthaultii, Solanum chacoense* and *Solanum tarijense,* respectively (Smilde *et al.* 2005, Jones *et al.* 2007, Foster *et al.* 2009, Park *et al.* 2009, Pel *et al.* 2009, Vossen *et al.* 2009, Jones *et al.* 2014a).

R gene-mediated resistance is generally based on a strong hypersensitive response (HR), but in potato, single *R* genes have failed to provide durable resistance against late blight. Therefore, the modern breeding approach is to isolate a variation of *R* genes and deploy them in pyramids. This is expected to lead to broad-spectrum recognition of *P. infestans* isolates and might provide a more durable resistance (Jo *et al.* 2016). The originally laborious job of cloning new *R* genes has accelerated in recent years. Map-based cloning approaches have been greatly facilitated