

## Ptr1: a case study of convergent evolution of AvrRpt2 recognition in diverse solanaceous species

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Race 1 strains of *Pseudomonas syringae* pv. tomato (*Pst*), which cause bacterial speck disease of tomato, are becoming increasingly common and no simply-inherited genetic resistance to such strains is known. We discovered that a locus in Solanum lycopersicoides, termed Pseudomonas tomato race 1 (Ptr1), confers resistance to race 1 Pst strains by recognizing the type III effector AvrRpt2. In Arabidopsis and apple, strains of Pst and Erwinia amylovora expressing AvrRpt2 degrade the RIN4 protein thereby activating RPS2 or Mr5-mediated immunity, respectively. Ptr1 also recognized homologs of AvrRpt2 from diverse bacteria including *Ralstonia pseudosolanacearum* strains expressing RipBN, and this correlated with the ability of AvrRpt2 homologs to degrade RIN4. Using site-directed mutagenesis of AvrRpt2 we found that, like RPS2, activation of Ptr1 requires AvrRpt2 proteolytic activity. The identification of the Ptr1 candidates from a pool of segregating F2 plants for the Ptr1 locus followed by the analysis of gene models in the S. lycopersicoides genome sequence and RNA-Seq data led to two nucleotide-binding leucine-rich repeat protein (NLR)-encoding genes as the strongest candidates for Ptr1. One of these two candidates was found to encode Ptr1 based on its ability to mediate recognition of AvrRpt2 and RipBN when it was transiently expressed with these effectors in leaves of Nicotiana glutinosa. The ortholog of Ptr1 in tomato and in Solanum pennellii is a pseudogene. However, a functional Ptr1 ortholog exists in Nicotiana benthamiana and potato, and both mediate recognition of AvrRpt2 and RipBN. In apple and Arabidopsis, recognition of AvrRpt2 is mediated by the Mr5 and RPS2 proteins, respectively. Phylogenetic analysis places Ptr1 in a distinct clade compared with Mr5 and RPS2, and it therefore appears to have arisen by convergent evolution for recognition of AvrRpt2. Ptr1 could play an important role in controlling bacterial speck disease, and its cloning is an example of convergent evolution for recognition of a widespread type III effector.