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Spotlight

Plant immune receptors can sequester and protect host proteins from pathogen-promoted degradation

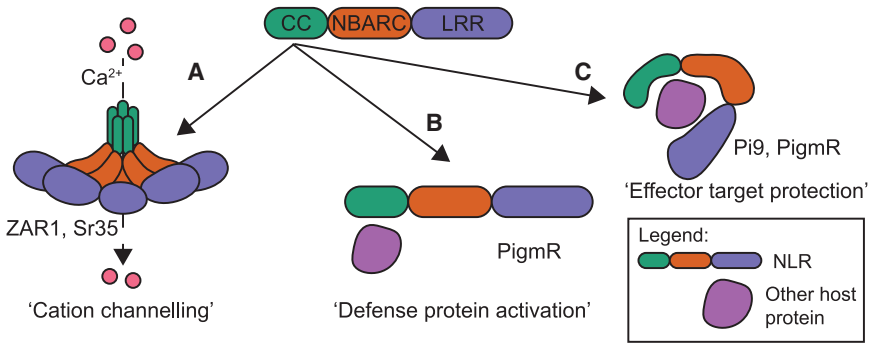

Figure 1. Action models of CC-type NLRs.
(A) Effector-activated NLRs such as ZAR1 (for HOPZ-ACTIVATED RESISTANCE 1) and Sr35 can form a Ca^{2+}-permeable cation pore (Förderer et al., 2022).
(B) CNLs can also activate host proteins via the CC domain, as an example, for defense-promoting TF activity (Zhai et al., 2019).
(C) CNLs such as Pi9 and PigmR appear to also sequester host proteins away from the effector-promoted degradation (Zhai et al., 2022; Shi et al., 2023). This is distinct from the guard-guardee concept because the target protection does not imply NLR activation by the effector. CC, coiled-coil domain; NBARC, nucleotide-binding domain shared by APAF-1, certain R gene products, and CED-4; LRR, leucine-rich repeats domain.

Genetically controlled broad-spectrum disease resistance is a highly desired trait for crop improvement. It allows us to reduce the use of pesticides in the field and helps to streamline the development of new varieties. More than 100 loci are known to control the resistance of rice (*Oryza sativa*) to the devastating fungal blast disease caused by *Magnaporthe oryzae*. Some of these loci are effective against a small set of pathogen isolates, while others protect against a broader range of pathogen variants (Ning et al., 2020).

Multiple broadly effective blast resistance genes encode for intracellular immune receptors with nucleotide-binding and leucine-rich repeat domains (NLRs). Usually, NLRs recognize effectors, which are virulence proteins produced by pathogens, and activate a range of defense reactions. One of the most effective blast NLR resistance genes is *Pi9*, which is homologous and genetically linked to other broad-spectrum blast resistance genes such as *Piz-t* and *PigmR* (Qu et al., 2006). It confers effective resistance against AvrPi9-containing blast isolates (Wu et al., 2015). Studies of Pi9-like NLRs have led to important contributions to the field of plant immunology such as the tissue-specific control of the NLR expression (Deng et al., 2017), growth-defense trade-off (Deng et al., 2017; Shi et al., 2023), the connection of effector recognition to the transcriptional control of defense (Zhai et al., 2019), and hormone production (Zhai et al., 2022). Still, mechanisms of Pi9 resistance remain poorly understood. Shi and colleagues (Shi et al., 2023) provided new insight into the Pi9 activity and gave evidence for a new model of NLR functioning.

To investigate mechanisms of the Pi9 resistance, Shi and colleagues (Shi et al., 2023) started looking at the Pi9 and AvrPi9 physical interactions. Since direct interactions between Pi9 and its matching effector, AvrPi9, could not be detected (Wu et al., 2015; Shi et al., 2023), the authors searched for other AvrPi9 interactors and found a conserved plant protein called ANIP1 (AvrPi9-interacting protein 1). It has the ubiquitin-like domain present in proteins forming complexes with the 26S proteasome. Consistently, ANIP1 interacted with components of the regulatory subunit of the 26S proteasome and was less stable (~10 min half-life time) in the absence of the 26S proteasome inhibitor. Search for the ANIP1 degradation targets identified a rice defense-promoting transcription factor (TF) *Os*WRKY62 whose degradation was further enhanced by AvrPi9. Interestingly, *Os*WRKY62 was stabilized in the presence of NLR Pi9. This observation could have fit a model where the effector AvrPi9 promotes the degradation of *Os*WRKY62 and NLR Pi9 prevents this, leading to *OsWRKY62*-dependent defense. In contrast to these predictions and despite positive regulation of blast resistance by *OsWRKY62* in the absence of *Pi9*, *OsWRKY62* contributed to susceptibility to, and not resistance against, the blast fungus when Pi9 was present. Thus, Pi9 appears to protect *Os*WRKY62 from degradation independently of its effector recognition function.

Although the jewelry on the Pi9 activation by AvrPi9 is still out, the study by Shi et al. (2023) points to a new aspect of the plant NLR biology (Figure 1). Usually, the activity of receptor coiled-coil NLRs (CNLs) is directly or indirectly triggered by effectors leading to the CNL cation pore formation (Figure 1A) or activation of defense-promoting host factors, for instance TFs (Figure 1B; Zhai et al., 2019; Förderer et al., 2022). In the study

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by Shi et al. (2023), it was shown that an NLR can also sequester a host TF to protect it from degradation, thereby probably increasing basal defense levels against the pathogen (Figure 1C). This phenomenon of the effector target protection aligns with a recent study where PigmR, a Pi9 homolog, interferes with an effector AvrPi9-stimulated degradation of a host deubiquitinase and thereby supports the synthesis of the defense hormone ethylene (Zhai et al., 2022).

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