

# Plant NLRs: The Whistleblowers of Plant Immunity

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In the NRC subsection of this review, there are several sentences with reference errors or misleading wording. These sentences are contained within the paragraph “There are four subclades in the NRC family, namely *NRC1*, *NRC2*, *NRC3*, and *NRC4*. *NRC1* was first observed in a *Solanum lycopersicum* screen.... The complexity of the NRCs will be better explained upon further biochemical and genetic analysis.” The authors of this review request the publication of the corrected paragraph as follows:

“There are four subclades in the NRC family, namely *NRC1*, *NRC2*, *NRC3*, and *NRC4*. *NRC1* was first identified in a *Solanum lycopersicum* virus induced gene silencing (VIGS) screen for genes required for Cf-4 function (Gabriëls et al., 2006). When VIGS was performed with an *NRC1* gene fragment from *S. lycopersicum* to silence *NRC1* in *N. benthamiana* (Gabriëls et al., 2006, Gabriëls et al., 2007), immune response triggered by R proteins Pto, Cf4, Cf-9, Ve1, Rx, LeEix2, and Mi were attenuated (Gabriëls et al., 2006, Gabriëls et al., 2007). However, more recent studies found that *N. benthamiana* does not have an *NRC1* ortholog, and instead carries a number of *NRC1* paralogs, which were termed *NRC2a*, *NRC2b*, *NRC2c*, *NRC3*, and *NRC4* (Wu et al., 2016, Wu et al., 2017). When the initial gene fragment from the VIGS experiments was analyzed, it was predicted that the fragment would likely have targeted the *N. benthamiana* genes *NRC2a*, *NRC2b*, *NRC2c*, and *NRC3* (Wu et al., 2016). *NRC2a*, *NRC2b*, and *NRC3* are required for Prf, R8, and Pto-mediated HR, and are weakly involved in Cf4-mediated HR, contributing redundantly to Rx-mediated immunity alongside *NRC4* (Wu et al., 2016, Wu et al., 2017). On the other hand, *NRC4* was found to be required for HR mediated by Rpi-blb2, R1, and Mi-1.2 in *N. benthamiana* (Wu et al., 2017). *NRC4*'s p-loop is essential in the *N. benthamiana* HR responses, whereas the CC domain was sufficient for immunity (Wu et al., 2017), as defense could be enhanced in *S. lycopersicum* by truncating *NRC4* by 67 amino acids using CRISPR/Cas9 editing (Leibman-Markus et al., 2018a, Leibman-Markus et al., 2018b). Triple silencing of *NRC2*, *NRC3*, and *NRC4* in *N. benthamiana* lead to disruption of Rx, R1, R8, Mi-1.2, Sw5b, and Bs2-mediated HR (Wu et al., 2017). Thus, the NRC family members seem to have evolved to serve redundant convergent helper roles for a large repertoire of sensor NLRs recognizing diverse effectors from viruses, bacteria, oomycetes, nematodes, and insects. Future biochemical analysis will be needed to reveal how these helper NLRs work alongside other proteins to signal defense responses in Solanaceae.”

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