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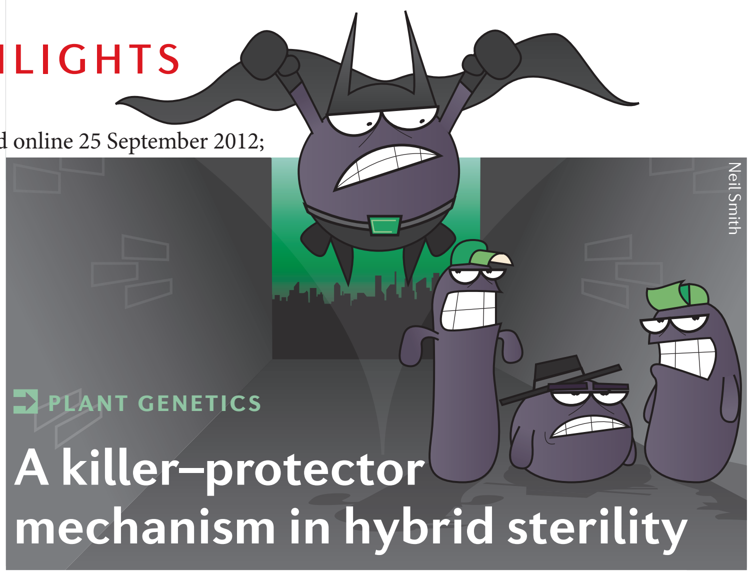

PLANT GENETICS

A killer–protector mechanism in hybrid sterility

Hybrid sterility maintains species identity by restricting gene flow between species. Recently, Yang *et al.* have elucidated for the first time a molecular mechanism by which hybrid sterility is mediated. They identified three genes that interact in a killer–protector system to regulate sterility in a hybrid of the *indica* and *japonica* subspecies of cultivated rice (*Oryza sativa* L.).

The authors focused on the S5 locus, which has previously been shown to be required for sterility in *indica–japonica* hybrids. Upon crossing the two subspecies, they found that there was a segregation distortion of the *indica* (S5-i) and *japonica* (S5-j) genotypes when crossing the two lines, with the preferential transmission of the *indica* genotype.

To try to explain both the segregation distortion and the hybrid sterility, the authors sequenced the S5 locus in the strains Nanjing 11 (*indica*), Balilla (*japonica*), Dular and 02428, the latter two both being widely compatible strains. For three of the ORFs that lie in the S5 locus — *ORF3*, *ORF4* and *ORF5* — the authors were able to predict whether the versions of these ORFs present in the different subspecies were likely to be functional or otherwise. They designated the predicted malfunctioning ORFs with '–' and the predicted functioning ORFs with '+'. Previously, transformation of plants with *ORF5+* from an *indica ORF5+* variety to a *japonica ORF5–* variety showed that *ORF5+* was able to decrease fertility. Here, the authors crossed *ORF3+* transformed lines, revealing that *ORF3+* was able to rescue fertility in *indica–japonica* hybrids, presumably by providing 'protection' from *ORF5+*. By breeding lines that differed only in their *ORF4+* or *ORF4–* status, the authors also showed that *ORF4+* is indispensable for gamete killing and hence that it cooperates with *ORF5+*.

In order to further characterize this killer–protector mechanism, Yang *et al.* expressed transgenes carrying these ORFs in relevant tissues and examined their subcellular localizations. They also assessed gene expression changes and programmed cell death (PCD) in ovaries in response to *ORF5+*.

The authors' results suggest that extracellular *ORF5+* induces endoplasmic reticulum stress via plasma membrane signalling of *ORF4+*. This in turn triggers the alternative splicing of the transcription factor *BZIP50*, which results in the expression of *ORF3*. The result of this *ORF3* expression is protection from PCD in the ovaries of *ORF3+* but not *ORF3–* plants. In the absence of this protection, embryo-sac abortion takes place, which also results in the preferential transmission of the *indica ORF3+* gene.

Sequencing data from 82 accessions of rice suggest that this mechanism is widespread even in wild rice. Hence this reproductive isolation mechanism may have had a profound influence on the evolution and diversification of rice and could be manipulated in rice breeding programmes. It remains to be seen whether similar mechanisms underlie hybrid sterility in other plant species.

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ORIGINAL RESEARCH PAPER Yang, J. *et al.* A killer-protector system regulates both hybrid sterility and segregation distortion in rice. *Science* **337**, 1336–1340 (2012)