

Understanding and breaking down the reproductive barrier between Asian and African cultivated rice: a new start for hybrid rice breeding

Yidan Ouyang^{*}

National Key Laboratory of Crop Genetic Improvement and National Centre of Plant Gene Research (Wuhan),
Huazhong Agricultural University, Wuhan 430070, China

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Oryza sativa and *O. glaberrima*, commonly known as Asian and African cultivated rice, are two domesticated rice species in *Oryza* genus. Asian cultivated rice may produce higher yields with better quality, whereas African cultivated rice shows a wide range of tolerance to abiotic and biotic stresses. Interspecific hybrids between *O. sativa* and *O. glaberrima* would show strong heterosis and thus increasing production because of their distant genetic diversity and complementary agronomic traits. However, reduced fertility is observed in hybrids from interspecific crosses; this hinders further utilization of rice heterosis in agriculture production. Such severe abnormal development of gametophytes in hybrids is caused by reproductive isolation, a process that prevents individuals of genetically diverged groups from mating, survival or producing fertile offspring. These reproductive barriers would drive speciation and maintain species identity by restriction of gene flow between differentiated populations. Therefore, understanding the genetic and molecular basis of reproductive isolation represents a fundamental concern in evolutionary biology.

Near thirty years after the first glimpse of the reproductive barrier between *O. sativa* and *O. glaberrima* (Sano, 1990), the genetic factors regulating incompatibility between these two cultivated rice species have now been unveiled. The *SI* locus is an important speciation locus as it affects both male

and female sterility in hybrids from such interspecific crosses. Genetically, the gametes carrying *SI* alleles from Asian rice are selectively eliminated, leading to preferential transmission of the African alleles at *SI* locus and consequently male and female sterilities in the heterozygotes. By a first glance of the causal gene(s) responsible for *SI* locus two years ago, researchers from South China Agricultural University and their collaborators identified the involvement of an *O. glaberrima*-divergent gene *OgTPR1* in *SI*-mediated hybrid sterility (Xie et al., 2017), followed by identification of another *O. glaberrima*-specific peptidase-coding gene *SSP* at *SI* locus by Koide and his colleagues (Koide et al., 2018). A complete understanding of such Asian-African reproductive barrier has now been released by the same team in South China Agricultural University and their collaborators (Xie et al., 2019a). In this study, they identified a classical killer-protector system driving an extremely asymmetric allelic interaction in interspecific rice hybrids. Three tightly linked genes in the African rice allele *SI-g*, *SIA4*, *SITPR* (*OgTPR1* mentioned in the previous study by Xie et al. 2017), and *SIA6* (*SSP* mentioned in the previous study by Koide et al. 2018), constitute a functional killer that triggers a sterility signal in sporophytic meiotic cells, which selectively eliminates both male and female gametes without the African rice gene *SITPR*, thus leading to reduced fertility and segregation distortion in the offspring. A novel and interesting feature is that one of the causal genes, *SITPR*,

^{*}Corresponding author (email: diana1983941@mail.hzau.edu.cn)

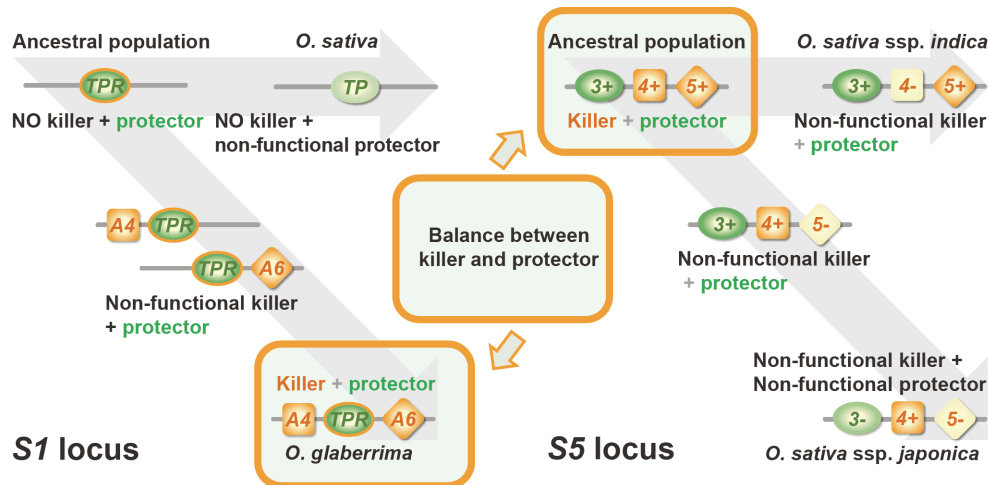


Figure 1 Turnover of the gamete killer-protector balance under parallel-sequential divergence determines the reproductive barriers mediated by *S1* and *S5*. *A4*, *A6*, *TPR*, and *TP* indicate *SIA4*, *SIA6*, *SITPR*, and *SITP* at *S1* locus, while 3, 4, and 5 indicate *ORF3*, *ORF4*, and *ORF5* at *S5* locus.

which acts as a component of the gamete-kill complex in hybrids at sporophytic stage, is also responsible for rescuing the gametes in a gametophytic manner. These findings confirm that complex loci composed of multiple closely linked genes are common for hybrid sterility (Xie et al. 2019b). This work substantially expands our understanding of reproductive isolation, and it also indicates that the generation of different killer-protector systems may be a general strategy for postzygotic reproductive isolation during the evolution.

The evolutionary route of *S1* also provides fresh data in understanding a complex reproductive isolation system with more than two components (Xie et al., 2019a). The common ancestor of the grass family only contained a single *SITPR* gene at the *S1* locus (Figure 1). In one lineage of the *Oryza* genus, the newly emerged *SITP* alleles were diverged from the ancestral *SITPR* by nucleotide variations and were further fixed in *O. rufipogon* and *O. sativa*; this behaved as a critical step for the origin of *S1* reproductive barrier. Meanwhile, a number of intermediate products, including *SIA4-SITP* and *SITP-SIA6*, were generated in the *Oryza* gene pool, along with *de novo* origination of two new genes *SIA4* and *SIA6* flanking *SITP*. Two other major steps for the emergence of *S1*-mediated hybrid sterility occurred in another parallel lineage with *O. barthii* and *O. glaberrima*. Intermediate recombinants of *SIA4-SITPR* and *SITPR-SIA6* were firstly generated by occasional hybridization, although such divergence of *S1* in ancient rice species was still insufficient to induce hybrid incompatibility. Subsequently, the three-gene fragment of *SIA4-SITPR-SIA6* that arisen from recombination of *SIA4-SITPR* and *SITPR-SIA6* determined the establishment of reproductive isolation at *S1*. The evolutionary trajectory of *S1* could be decomposed into the parallel divergence of the gamete-protector (i.e., *SITPR*)

between African and Asian rice lineages, and sequential origination of the functional gamete-killer (i.e., *SIA4-SITPR-SIA6*) following hybridization of the intermediate recombinants in African rice lineage (*O. barthii* and *O. glaberrima*); this expands the generality of the parallel-sequential divergence model for reproductive isolation by involving three genes (Ouyang and Zhang, 2013). What should also be mentioned in particular is that at *S1* locus, the establishment of the reproductive barrier is determined by the formation of co-existence of gamete killer and protector during the evolution; this is completely opposite to the origin of another three-gene reproductive isolation system *S5*, which is caused by breaking down of the balance between killer and protector in the ancestral population (Figure 1) (Ouyang et al., 2016; Yang et al., 2012).

Consequently, the *S1-n* alleles, i.e., the compatible genotypes that are able to overcome hybrid sterility between *O. sativa* and *O. glaberrima*, can be deduced based on the genetic and evolutionary picture of *S1*. These neutral haplotypes are predicted to be ones with a functional protector *SITPR* and at least one non-functional component of the killer; they are assumed to originate in the African rice lineage. Compatible varieties with *S1-n* allele can thus be created using the CRISPR/Cas9 system or natural mutation either by disrupting *SITPR*, *SIA4*, or *SIA6/SSP* (or their combination) in African rice; these materials would undoubtedly produce fertile hybrids when crossed with either African or Asian rice (Koide et al., 2018; Xie et al., 2017, 2019a). We believe that the progress in *S1* may serve the first step for a feasible approach to overcome the interspecific reproductive isolation, thereby facilitating the utilization of distant heterosis in Asian-African hybrid rice breeding.

Compliance and ethics The author(s) declare that they have no conflict of interest.

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