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RICE DOMESTICATION

An imperfect African solution

SHATTERING 4 is a key rice domestication gene. A non-synonymous mutation of this gene was found to be selected during Asian rice domestication as it confers non-shattering. Now, a nonsense mutation of *SHATTERING 4* is shown to simultaneously result in non-shattering and small grain size during the independent domestication of African rice.

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Crop domestication is an unrepeatable miracle in human history that underpins modern civilization. During domestication, humans selected larger grain size and loss of shattering to increase yield and facilitate harvest. As a consequence, cultivars typically have larger grains and reduced shattering habit compared with their wild relatives. However, African cultivated rice appears to be an exception, as it bears smaller grains than its progenitor. In the present issue of *Nature Plants*, Wu *et al.* found that a nonsense mutation within the gene *GRAIN LENGTH 4* (*GL4*), the orthologue of *SHATTERING 4* (*SH4*), simultaneously confers non-shattering and smaller grain size in African cultivated rice[1].

To identify the gene controlling grain length in African rice (*Oryza glaberrima* Steud.), the researchers used segregating populations and quantitative trait locus analysis to map a locus, *GL4*, which was further narrowed down to a single gene. Multiple independent transgenic complement experiments validated the function of the *GL4* gene in affecting grain size. A causal nonsense mutation was uncovered to account for the small grain size of African rice. The mutation causes a truncation of amino acid sequences with a nuclear localization signal (NLS) and disrupts the subcellular localization of the GL4 protein.

Unexpectedly, *GL4* was found to be the orthologue of the *SH4*/*SHATTERING 1* (*SHA1*) gene in Asian rice (*Oryza sativa* L.), which has been well-documented to control the loss of shattering during Asian rice domestication[2,3]. Compared with the Asian rice loss-of-function allele *sh4* (Fig. 1a,b), the nonsense mutation in *GL4* makes the seeds much harder to shed owing to a remarkable deficiency of abscission zone, and results in smaller grains. The mutant allele underwent a strong positive selection during domestication, but has not been fixed as the ancestral allele is still present in a minor proportion (~12%) of the cultivated accessions distributed around the domestication centre. The function of *GL4* on seed shattering has also been reported recently by Win *et al.*[4]. In that study, the hybrids of domesticated Asian and African rice demonstrated a throwback shattering phenotype with normal grain size (Fig. 1c).

While the study on *GL4* provides a good piece of evidence for the separate domestication of rice in West Africa[5], new questions arise as a result. The disruption of the potential interaction with other gene products at the C terminal of *GL4*/*SH4* probably caused the additional effect on grain size[1,4]. However, the molecular mechanisms remain unclear, and it is also puzzling that small grain size was selected. Is it an inevitable consequence of the

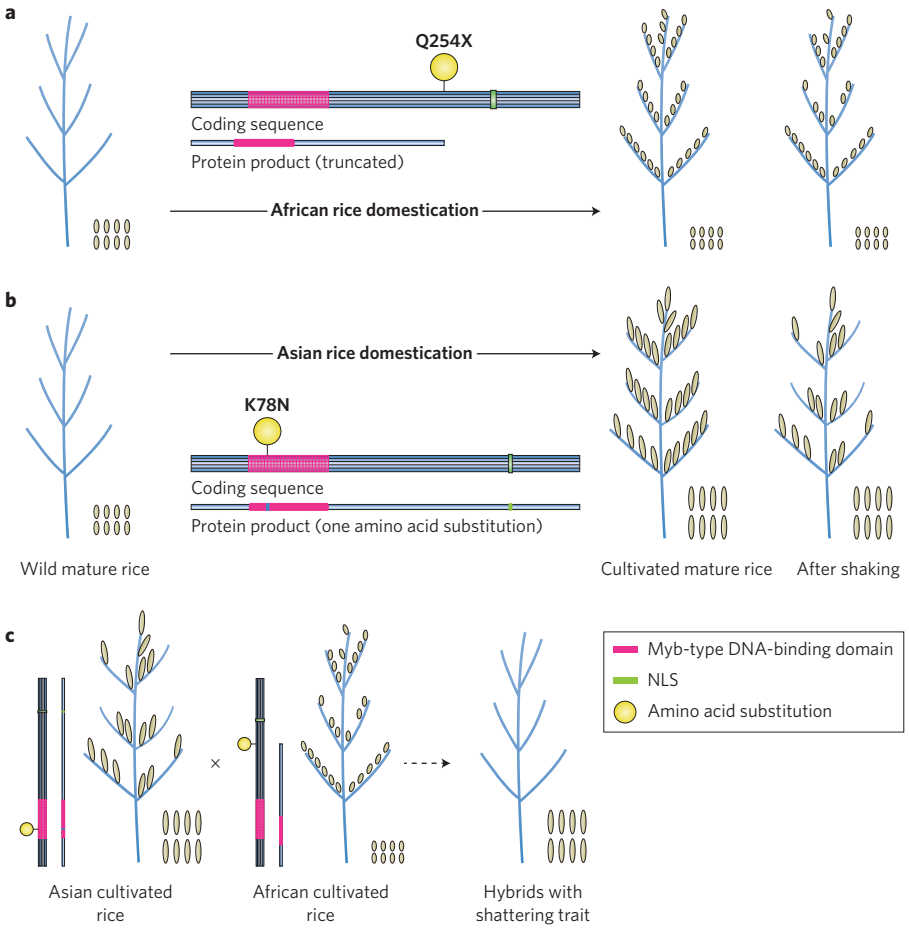

Figure 1 | Mutations at the *GL4*/*SH4* locus contribute to the parallel domestication of African and Asian rice. **a**, The nonsense mutation in African cultivated rice that led to the loss of the NLS results in a non-shattering phenotype and smaller grains. **b**, One amino acid substitution that occurred in the DNA-binding domain of the *GL4*/*SH4* product in Asian domesticated rice results in a non-shattering phenotype and normal grain size. **c**, The hybrids of the Asian and African cultivated rice demonstrate the wild-type shattering phenotype with normal grain size[4].

selection for non-shattering? And why has the *gl4* domestication allele not been fixed in African cultivars? Are there any other loci controlling non-shattering, or other mutant alleles of *GL4* to be detected in African rice? In relation to the study by Win *et al.*, further uncertainty comes from how the combination of the two cultivated alleles of *sh4* in heterozygotes results in wild phenotypes for shattering[4] (Fig. 1c). These questions require further study.

The selection of different *sh4* alleles to produce the non-shattering characteristic in domesticated Asian and African rice reminds us again that genetic heterogeneity exists extensively in parallel evolution, perhaps due to the high possibility that similar traits could result from independent mutations in one gene or functionally related genes. The independent selection of *gl4*/*sh4* alleles in two geographically separated rice species demonstrated that different genetic mutations bring similar, but not identical, consequences.

Identification of domestication genes is appealing not only because they help us to understand crop evolutionary histories, but also due to the potential application value of the genes. In fact, the developmental processes and relevant genes involved in loss of seed/fruit shattering have been revealed as highly conserved among many independently domesticated plants[6]. However, the present work reported for the first time the pleiotropic effects of *GL4*/*SH4* on shattering and grain size, with valuable implications for yield improvement. Replacing the African *gl4* allele with the Asian *sh4* allele would be a practicable breeding route to increasing grain yields of African rice. ❐

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References

1. Wu, W. *et al. Nat. Plants* **3,** 17064 (2017).
2. Li, C., Zhou, A. & Sang, T. *Science* **311,** 1936–1939 (2006).
3. Lin, Z. *et al. Planta* **226,** 11–20 (2007).
4. Win, K. T. *et al. New Phytol.* **213,** 1925–1935 (2017).
5. Wang, M. *et al. Nat. Genet.* **46,** 982–988 (2014).
6. Dong, Y. & Wang, Y. *Front. Plant Sci.* **6,** 476 (2015).

Competing interests

The authors declare no competing financial interests.