

How can rice genetics benefit from rice-domestication study?

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Uncovering the puzzle of the origin and domestication process of cultivated rice has greatly impacted rice genetics, but comprehensively exploiting elite alleles from both wild species and domesticated varieties for modern rice breeding is still a long-term ongoing study.

Crop domestication is one of the greatest innovations in human civilization. Understanding the origin and domestication process of cultivated rice is very important in profiling the history of agriculture. Modern cultivars have many morphological and physiological differences compared with their progenitors. Domesticated cultivars have obtained many beneficial alleles from their progenitors to adapt to local environmental conditions and control domestication alterations.

Asian cultivated rice, *Oryza sativa* L., has been domesticated from its ancestor, the wild-rice species *O. rufipogon*. As it is one of the most important food crops, rice cultivation has been deeply influenced by human civilization development [1]. *O. sativa* varieties and their progenitors are mainly cultivated in temperate, subtropical and tropical zones. *O. sativa* has two primary subspecies: *indica* and *japonica*. According to the analyses of genetic distance and population structure, *japonica* can be further divided into *temperate japonica* and *tropical japonica* subgroups [2]. Uncovering the process of rice domestication could give a better understanding of the nature of artificial selection and propose a model to be applied to the domestication studies of other crop species.

RICE-DOMESTICATION STUDIES BASED ON DOMESTICATED GENES

The process of rice domestication is closely linked with human conscious or unconscious selection and other forces. This process could be described as humans selecting and retaining the favored elite traits according to their selection (Table 1). The resulting domesticated plants therefore have larger seeds, higher resource allocation, more determinate growth and apical dominance, and non-shattering seeds compared with their ancestors. Genetic analysis of the domesticated genes and archaeological records could provide sufficient evidence to uncover the truth of cultivated-rice origin.

In past studies, efforts 'from phenotype to genes' help to identify many domestication-associated genes through quantitative trait locus (QTL) mapping. In maize, *Teosinte branched1 (tb1)* is the first identified domestication gene

controlling the difference in apical dominance compared with its progenitor, teosinte [3]. Higher expression patterns in maize are believed to result from artificial selections. In rice, some favored domestication genes have been characterized. Shattering is a notable domestication trait that could be easily selected by our ancestors and has directly contributed to crop yield. *qSH1* is a major QTL controlling shattering, encoding a homeobox-containing transcription factor. The causative mutation is a single nucleotide in a *cis*-regulatory element, regulating the shattering zone [4]. *sh4* is another major QTL controlling shattering that encodes a gene with homology to Myb3 transcription factors, and a single amino change in the DNA-binding domain causes rice to gain the trait of non-shattering [5]. There are many domestication genes relevant to domestication traits, such as *Bh4*, *PROG1*, *qSWS*, *An-1*, *An-2* and *Osc1*, which have been characterized up to date.

Table 1. The difference between favored domestication traits in *O. rufipogon* and *O. sativa*.

Domestication traits	<i>O. rufipogon</i>	<i>O. sativa</i>	Cloned gene(s)
Shattering	Strong	Weak	<i>Sh4, qsh1</i>
Hull color	Most are black	Most are yellow	<i>Bh4</i>
Seed dormancy	High	Low	<i>Sdr4</i>
Grain size	Smaller	Bigger	<i>qsw5</i>
Grain quality	High amylose	Low amylose	<i>Waxy</i>
Awn length	Long	Short or none	<i>An-1, An-2</i>
Tiller angle	Prostrate growth and wider tiller angle	Erected growth and narrower tiller angle	<i>PROG1</i>
Panicle shape	Dispersed	Closed	<i>OsLG1</i>
Germination rate	Low	High	–
Stigma exertion	Yes	No	–

Archaeological evidence has shown that rice domestication began in the Yangtze Valley in China about 8000–9000 years ago and it was cultivated early in the Ganges in India about 4000 years ago [6]. The earlier human-cultivation practice was during the hunter-gatherers' lives. Human ancestors tried to improve wild cereal crop to meet their needs and make the beneficial domestication genes inherited from its progenitor. Archaeological records provide evidence that seed-size enlargement can occur before the loss of shattering. In wheat and barley, archaeological studies demonstrated that an increase in grain size was followed by the fixation of non-shattering rachises [7]. Based on the genetic and archaeological evidence, many studies addressed the origin of cultivated rice. The most recent genetic studies tended to support the single-origin model through genetic characterization of the key domestication genes. Rice single-origin theory, the snowball model, demonstrated that the earlier critical domestication gene was first introduced to other regions of Asia, and the introgression occurred between the cultivar and local populations of *O. nivara* and *O. rufipogon*. The multiple-origin model from their perspective was a combination model. In this model, there were multiple mutations existing in divergent wild populations, and the key domestication genes between *indica* and *japonica* were formed by hybridization between the subspecies after their independent domestications [8].

RICE DOMESTICATION: A SINGLE ORIGIN AND MULTIPLE INTROGRESSIONS

Population genetics study in crops showed that the causative mutation in a domestication gene is fixed in the cultivars, causing decreased genetic diversity, which is called 'selective sweeps'. Recent comprehensive study on rice genome variations of wild-rice *O. rufipogon* accessions and cultivated-rice *O. sativa* varieties has provided solid evidence to investigate the phylogenetic relationships between cultivated and wild rice, and identified the signatures

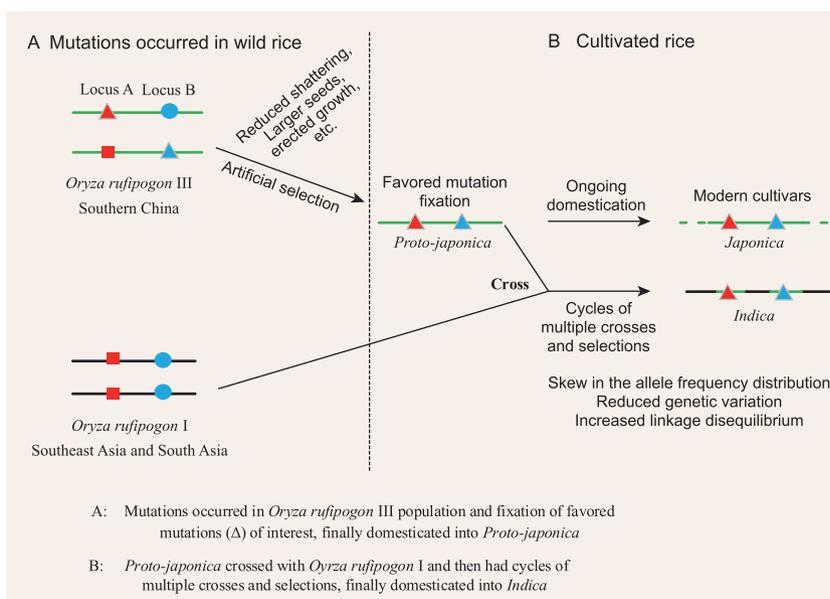


Figure 1. The domestication process of two main *O. sativa* subspecies: *indica* and *japonica*. The data are from the analysis of 55 selective sweeps involved in the Asia rice domestication [9]. The process can be divided into two parts: A and B. (A) Locus A (the red filled triangle and square indicate the two types of allele) and Locus B (the blue filled triangle and circle indicate the two types of allele) represent two genes regarding domestication syndromes, such as reduced shattering, larger seeds, erected growth, etc. The green and black thick lines represent different backgrounds of *O. rufipogon* III and *O. rufipogon* I, respectively. Mutations of Locus A and Locus B that randomly occurred in the *O. rufipogon* III population (from southern China) were favorably selected as domestication genes are indicated by filled triangles. (B) The *proto-japonica* varieties were domesticated from *O. rufipogon* III. The *indica* varieties were subsequently domesticated through crosses between the *proto-japonica* and *O. rufipogon* I (from south-east Asia and south Asia) after many cycles of multiple crosses and selections. During this process, the important signatures can lead to the conclusion of a skew in the allele frequency distribution, reduced genetic variation and increased linkage disequilibrium.

of selection in rice domestication. This systematic comparison identified 55 selective sweeps that were involved in domestication [9]. If a gene was related to a domestication trait, then it might show a decrease in nucleotide diversity, increased linkage disequilibrium (LD) and altered population frequencies of polymorphic nucleotides in the gene and linked regions, which can provide sufficient evidence to manifest rice origin and domestication.

Based on rice genome variation studies, cultivated rice is found to undergo a single origin and multiple introgressions. Some useful mutations might have randomly occurred in some populations of wild-rice species, and were then selected and fixed for generating the *proto-japonica*-like varieties. The *proto-japonica*-like varieties were farther spread to other places in Asia.

The *indica* varieties were subsequently generated through the crosses between the *proto-japonica*-like varieties and the *O. rufipogon* lines in local regions after many cycles of crosses and selections (Fig. 1). The favored mutations that have been fixed with their flanking regions of low genetic diversity (selective sweeps) in cultivated rice provide strong evidence to trace their origins.

RICE DOMESTICATION BENEFITS RICE BREEDING AND FUNCTIONAL GENOMICS STUDIES

Genetic studies on domestication may provide some guidance for future breeding. Improving grain production and quality is an ongoing effort in crop breeding. To meet the challenges of global

climate changes, a new expectation of high grain production has arisen in crop production. More and more beneficial gene alleles underlying specific traits have been selected in modern breeding [10]. The high yield and high grain quality of modern cultivars were contributed by the combination of many domestication- and improvement-related genes.

The great diversity in wild-rice populations, which have much more natural allelic variation than domesticated rice (especially the modern cultivars), will facilitate breeding to improve performance in many agronomic traits, including pathogen resistance and abiotic-stress tolerance. Uncovering the origin of cultivated rice has formed a solid foundation for a comprehensive identification of the genetic diversity in wild rice, landraces and elite varieties, and provided useful resources for the characterization of the genetic mechanism of agronomically important traits. The sig-

nificantly reduced genetic diversity in cultivated rice is a limitation for further rice genetic improvement and the high level of allelic variation in wild rice will be an important resource in designed rice breeding that can be reintroduced into the gene pools of current elite varieties. Taken together, both the rice-domestication studies and the comprehensive analyses of genetic variation in rice will greatly benefit the studies of rice gene function in agronomical traits.

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National Science Review
3: 278–280, 2016
doi: 10.1093/nsr/nww039

BIOLOGY & BIOCHEMISTRY

Special Topic: Rice Breeding

Starch metabolism and grain chalkiness under high temperature stress

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Rice is one of the most important staple crops, demand for which is increasing with population growth all over the world, especially in Asia. Because of recent global warming, significant reduction in yield and quality of rice has now become a serious problem. One of the most common damages incurred by high temperature (HT) stress is grain chalkiness. Chalky grains show loosely packed starch granules and large air spaces in the endosperm, accounting for an increase in brittleness that consequently leads to great losses in grain yield and reduction in palatability as a result of changes in amylose contents, chain length distributions of amylopectin and storage

protein contents [1,2]. Therefore, it has become important to study the mechanism of starch metabolism and formation of HT-induced chalkiness. Starch is composed of two types of molecules: linear and helical amyloses containing α -1,4-glycosidic bonds, and branched amylopectins containing both α -1,4- and α -1,6-glycosidic bonds. In rice endosperm, amylose is synthesized mainly by granule-bond starch synthase I (GBSSI/Wx); whereas amylopectin is synthesized by the joint action of soluble starch synthases (SSs), starch branching enzyme (BEs) and debranching enzymes (DBEs) [3] (Fig. 1). In this review, we reported the genetic components involved in grain

chalkiness and the recent success in quantitative trait loci (QTL) study of grain chalkiness.

DEFECTS IN STARCH SYNTHESIS UNDER HT STRESS CAUSE GRAIN CHALKINESS

As mentioned, GBSSI/Wx is the central enzyme for amylose synthesis and was identified as the causal gene for amylose content and gel consistency. Recently, Zhang *et al.* [4] showed that an increase in the splicing efficiency of GBSSI/Wx pre-mRNA might deal with maintaining amylose content under HT condition. A comprehensive study