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## An SNP caused loss of seed shattering during rice domestication

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Rice (*Oryza sativa*) is a staple food for human beings and it is believed that rice was domesticated around ten thousand years ago. It was long assumed that a single major domestication process occurred which produced a subspecies of rice and that subsequent artificial selection upon existing variation resulted in rice cultivar groups such as *indica*, tropical *japonica*, and temperate *japonica*. Recent genome analysis revealed that this assumption might be wrong because an *indica* cultivar '93-11' and a *japonica* cultivar 'Nipponbare' became diversified about 0.2-0.4 million years ago based on phylogenetic analyses of retrotransposon distribution. Therefore, several independent domestication processes may have occurred to make the diversity of these subspecies in rice. However, it is not well understood how the domestication process took place at the molecular level.

Here, we first performed QTL (quantitative trait locus) analysis for the seed shattering trait, one of the domestication traits, between an *indica* cultivar (Kasalath) and a *japonica* cultivar (Nipponbare) (Fig. 1) and detected five QTL loci involved in seed shattering. We next cloned a major gene termed *qSH1* (QTL of seed shattering in chromosome 1). *qSH1* encodes a Bell-type homeobox transcription factor which is an ortholog of *REPLUMLESS* (*RPL*) gene in *Arabidopsis thaliana*. *RPL* was reported to be involved in formation of the abscission layer in *A. thaliana* fruit. Indeed, a nearly isogenic line, NIL (*qSH1*), containing a Kasalath genome fragment corresponding to the *qSH1* region, restored formation of the separation layer at the bottom of rice grains which shattered easily (Fig. 2). These results indicate that *qSH1* is

required for the abscission layer formation in rice and, thus, revealed that an evolutionarily conserved molecular mechanism is involved in the separation layer formation regardless of the botanical origin of the layers.

Fine mapping of *qSH1* also led us to identify a single nucleotide polymorphism (SNP) which caused the loss of seed shattering. *In situ* expression analysis of *qSH1* mRNA (Fig. 3)

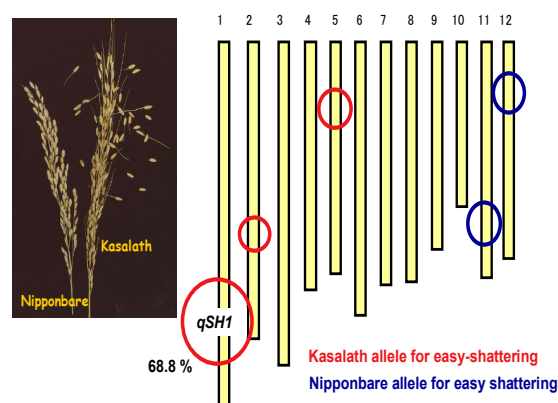


Fig. 1 Seed shattering habits of rice panicles (left) and chromosomal locations of QTLs for seed shattering degree (right)

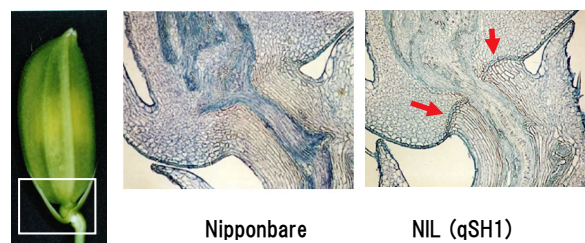


Fig. 2 Left: Photo of a rice grain. White box indicates position of abscission layer formation. Middle and right: Longitudinal sections of positions corresponding to white box. The corresponding region of Nipponbare (middle) and the completed abscission layer of NIL (*qSH1*) (right).



and complementation tests using 12 Kasalath genome fragments further demonstrated that this SNP conferred loss of abscission layer-specific transcription of *qSH1*. These results suggested that ancient humans likely selected this SNP for loss of seed shattering due to the defect in formation of the separation layer.

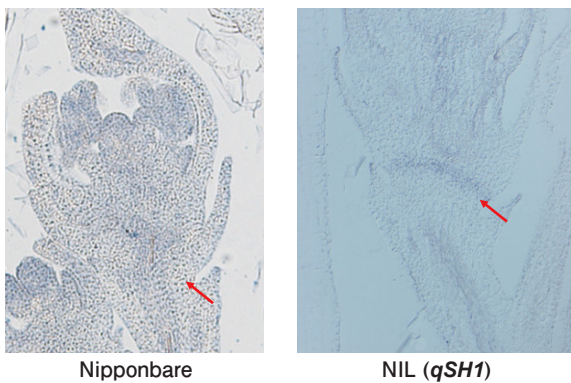
We further analyzed haplotypes of the *qSH1* gene using several rice core collections. These analyses revealed that the SNP was introduced into rice cultivars after the diversification of temperate *japonica*. When temperate *japonica* cultivars of Chinese origin were tested, we found that that the SNP was likely to have occurred as a mutation in ancient China. Since it is believed that rice cultivation was

introduced into Japan at least 3000 years ago, the mutation for SNP is likely to have occurred more than 3000 years ago.

Therefore, we finally concluded that the loss of seed shattering occurred in the early domestication of temperate *japonica* more than 3000 years ago and then ancient humans in China selected rice plants with this specific SNP to improve yields due to the decrease of seed dispersal (Fig. 4).

**Reference**

Konishi S, Izawa T, Lin S-Y, Ebana K, Fukuta Y, Sasaki T, Yano M (2006) An SNP caused loss of seed shattering during rice domestication. *Science*, **312**: 1392-1396.



**Fig. 3** In situ analysis of *qSH1* expression  
At flower formation stage, *qSH1* expression was detected in anther regions in both NIL(*qSH1*) and Nipponbare (left) and at the provisional abscission layer position only in NIL(*qSH1*) (right) and not in Nipponbare.



**Fig. 4** The origin of the identified SNP