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One gene's shattering effects

Kenneth M Olsen

A new study shows that three independent mutations in the *Sh1* gene, which encodes a YABBY transcription factor, gave rise to the non-shattering seed phenotype in domesticated sorghum. This same gene may have also had a role in the domestication of other cereals, including maize and rice.

The shift from freely shattering seeds, which easily fall off a plant at maturity, to non-shattering or reduced-shattering seeds represents a key transition during cereal crop domestication. Whereas wild grasses evolve under strong selection for the ability to disperse their seeds at maturity, domestication favors plants from which entire grain stalks can be efficiently harvested with minimal seed loss (Fig. 1a). However, once the shift to non-shattering grains occurs, the reproductive fate of a crop species becomes intimately tied to its human cultivators: subsequent crop generations depend on harvesting and reseed for their continued existence. In recent years, one of the major aims of crop domestication research has been to understand how non-shattering grains and other domestication traits evolved. Following pioneering work in the 1990s by John Doebley and colleagues in maize^{1,2}, studies in cereals and other crops have begun to resolve the genetic mechanisms underlying traits favored either during the initial stages of domestication (such as losses of seed shattering and dormancy) or during subsequent breeding for crop improvement (such as diversification in grain pigmentation and starch characteristics)³.

Only recently, however, have enough species and traits been examined that we can begin to ask whether the same genes underlie the same traits in different crop species. In this issue, Jianming Yu and colleagues⁴ make an important advance in addressing this question. Working in *Sorghum*, with comparative analyses in rice and maize, the authors identify the key gene responsible for non-shattering grains in domesticated sorghum, and they report evidence that orthologs of this gene may have

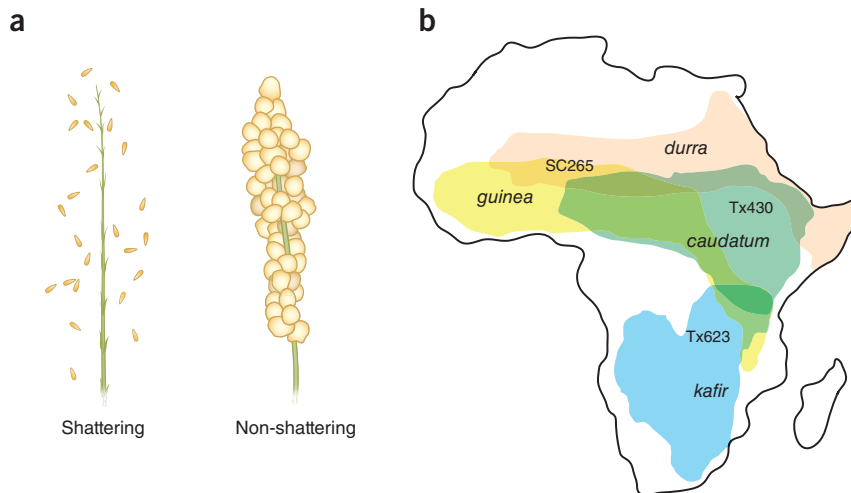


Figure 1 Multiple origins of non-shattering sorghum in Africa. (a) Shattering and non-shattering grains are characteristic of wild and domesticated varieties, respectively. After shaking, mature seeds scatter easily in shattering varieties. In contrast, seeds remain on the head of non-shattering varieties. (b) Approximate geographic distributions of sorghum varieties with *sh1* non-shattering alleles (SC265, Tx430, Tx623) among the major domesticated sorghum races in Africa: *durra* (light brown), *guinea* (yellow), *caudatum* (green) and *kafir* (blue). The *bicolor* sorghums (not shown) occur throughout the geographic range covered by the other crop forms.

contributed to the non-shattering phenotype in rice and maize as well.

Sorghum's multiple origins

Domesticated sorghum (*Sorghum bicolor*) provides a major source of calories for livestock and humans worldwide, with sorghum grain production ranking third among cereal crops in the United States and fifth globally. It is also considered to be an emerging bio-energy crop. Sorghum was domesticated in Africa, which still harbors a great diversity of cultivated forms. Five major morphological forms or 'races' have traditionally been recognized^{5,6}: *caudatum*, originating from eastern Africa; *durra*, predominant in the Horn of Africa and other arid regions; *guinea*, most characteristic of western Africa; *kafir*, dominant in subequatorial eastern Africa;

and the widely distributed *bicolor*, which includes both shattering and non-shattering varieties and is considered the most primitive form of the crop (Fig. 1b). A recent genome-wide analysis of SNP diversity confirmed the genetic distinctness of the four fully domesticated races⁶, a pattern potentially consistent with multiple independent domestication events.

Whereas in most crops shattering is controlled by many interacting genes, shattering in sorghum is controlled by a single major-effect quantitative trait locus (QTL)^{7,8}. In their new study, Lin *et al.*⁴ use map-based cloning to identify the causal gene, *Sh1*, which they find encodes a YABBY transcription factor. By sampling a large and diverse sorghum collection, the authors provide evidence that the non-shattering phenotype can be accounted for by

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one of three different loss-of-function alleles that were independently selected upon during domestication. Ten representative SNPs across the 11.8-kb *Sh1* gene define four haplotypes, one of which is characteristic of shattering samples and the other three of which are each present in a subset of the non-shattering domesticated forms. The three non-shattering haplotypes correspond broadly to sorghum races: SC265 predominates in *guinea* and *durra* varieties, Tx623 in *kafirs* and Tx430 in *caudatum* (Fig. 1b). Given the genome-wide differentiation occurring among the races, this pattern strongly suggests that sorghum underwent at least three independent episodes of selection for reduced shattering, each corresponding to a separate domestication event. This finding also leads to the prediction that the *Sh1* gene should bear signatures of selection reflecting three independent selective sweeps. To test this hypothesis, future work should include more detailed analysis of *Sh1* nucleotide variation (beyond the ten common SNPs examined in the current study), which should be compared to variation at unlinked loci. With expanded sampling of wild sorghum accessions, these *Sh1* sequences could also prove useful in identifying the specific wild populations that gave rise to the crop races.

Selection in other crops?

Foundational work by Andy Paterson and colleagues has previously shown that the genomic

location of the sorghum *Sh1* QTL corresponds to shattering QTLs in syntenic regions of the rice and maize genomes^{7,8}. This finding raised the intriguing possibility that the domestication of these different cereal crops might have occurred, at least in part, through parallel selection on the same underlying genetic target. With the *Sh1* gene now identified, Lin *et al.*⁴ were able to explore this possibility in greater detail. In rice, a non-shattering mutant was confirmed by the authors to have a loss-of-function mutation in the rice *Sh1* ortholog, *OsSh1*. Whereas *OsSh1* was not found to be one of the major domestication genes for reduced shattering in rice^{9,10}, it does correspond to a minor-effect QTL (for example, see ref. 11), and this locus has also been shown in genome-wide sequence analyses to have a potential signature of domestication-related selection^{12,13}. In maize, orthologs of *Sh1* were found to colocalize with two large-effect shattering QTLs in a mapping population derived from a cross of maize and its shattering ancestor, teosinte. In addition, the *Sh1* genomic region corresponds to a syntenic region in foxtail millet that contains a shattering QTL¹⁴. Thus, it seems that this *YABBY*-like gene may have been a shared target of selection for reduced shattering in several domesticated cereals. This finding is particularly interesting, given that shattering is a complex trait and is known to be controlled by multiple genetic factors in most crops. Closer examination of nucleotide variation

in the *Sh1* orthologs could be used to further explore this gene's role in the domestication of other cereals and to potentially identify any underlying causal mutations. More broadly, the study by Lin *et al.* adds *Sh1* to the list of genes encoding transcriptional regulators that a growing body of evidence suggests have been the key players in domestication-related morphological evolution³.

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