IN BRIEF

Domesticated versus Wild Rice? Bring It Awn!

By necessity, wild grasses are mean little things; for example, the seeds of many wild grass species have awns, large, barbed spikes that can fend off seed-eating animals, assist in seed dispersal, and help plant the seeds. In wheat (Triticum spp), changes in humidity cause the awns to flex, which can help bury the seeds. After thousands of years of artificial selection, our domesticated cereal crops have shorter or nonexistent awns to facilitate grain harvesting, handling, and storage. Rice (Oryza sativa) domestication also involved alterations in many traits, including growth habit, seed shattering, panicle architecture, grain size, and hull color (reviewed in Sang and Ge, 2013).

Domestication leaves many marks on the phenotype and, correspondingly, many marks on the genome (reviewed in Meyer and Purugganan, 2013). Different approaches, including examination of candidate genes, quantitative trait locus studies, and whole-genome resequencing have allowed researchers to identify domestication-related loci, such as An-1, which encodes a transcription factor related to awn length and grain yield in rice. To identify additional factors involved in awn formation, Hua et al. (2015) used genetic mapping to compare cultivated rice (O. sativa), which has short, barbless awns, and wild rice (Oryza rufipogon), which has long, barbed awns (see figure). This mapping identified LONG AND BARBED AWN1 (LABA1) as essential for awn formation in wild rice. They also used genetic complementation and RNA interference to confirm the role of LABA1 in awn formation.

Many domestication-related genes, including 37 of the 60 genes in the list compiled by Meyer and Purugganan (2013), encode transcription factors. By contrast, fewer loci encode enzymes, such as the classic domestication-related locus WAXY, which encodes a granule-bound starch synthase. Hua et al. showed that LABA1 encodes an enzyme involved in phytohormone biosynthesis. Comparisons to known enzymes and measurements of cytokinin levels in complemented plants indicated that LABA1 activates cytokinin by converting the inactive cytokinin nucleotide 5′-monophosphate to the active form. The authors also used in situ hybridization to show that in wild rice, LABA1 expression in the awn primordium promotes cell division and, thus, extension of the awn. By contrast, cultivated rice has a frame-shift mutation in LABA1, and the resulting lack of LABA1 reduces cytokinin in the awn primordia, causing the awns to fail to extend. Intriguingly, analysis of aus cultivars indicated that their barbless phenotype results from the action of a second gene, but identification of this factor remains for future research.

Sequencing in multiple cultivars showed that the laba1 allele occurs in many cultivated varieties of rice, but not in wild or African rice varieties, including O. rufipogon, Oryza glaberrima, and Oryza barthii. Most O. sativa cultivars contained the laba1 mutation, but some temperate japonica cultivars may lack awns due to a mutation in an-1, and some farmers may plant cultivars with awns to deter animal feeding. The laba1 allele likely originated in a japonica cultivar and was introgressed into indica cultivars. Genotyping and extended haplotype analysis showed low sequence diversity in an 800-kb region around the laba1 mutation, indicating strong selection, as might be expected for a domestication-related gene. Also consistent with its role in domestication, the awnless and barbless rice showed an increase in unit weight, measured as kg/m², indicating that the absence of the awn does indeed facilitate grain handling and storage.

Although domestication occurred very recently, at least on evolutionary time scales, many questions about the origins and phenotypes of rice cultivars remain. The identification of LABA1 provides intriguing insights on the role of cytokinins in awn development and the mechanisms by which humans tamed wild rice. It also leaves open intriguing questions on the contribution of LABA1 and other loci to the development of barbs.

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REFERENCES
