

What plant genes tell us about crop domestication

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The famous botanist George Beadle created a facsimile of an early of early domesticated corn (right) by crossing the wild grass teosinte (left) with Argentine popcorn. Credit: John Doebley

Anyone who has seen teosinte, the wild grass from which maize (corn) evolved, might be forgiven for assuming many genetic changes underlie the transformation of one plant to the other.

However, a method for exploring the genetics of domestication called Quantitative Trait Locus (QTL) mapping has revealed that only modest modifications are needed to convert a wild plant to a crop plant. Some major transitions in phenotype can even be achieved by a single [genetic change](#).

The few artificial experiments in domestication that have been conducted have also shown that it is possible to achieve domesticate-like plants in fewer than 20 generations.

None of this pleases archaeobotanists, who try to piece together the history of plant domestication from scraps of ancient plant remains.

Their data are sparse and unimpressive — a 10,000-year-old squash seed found in a cave in Oaxaca, Mexico, or four 12,000-year-old grains of rice recovered from a rock shelter in Hunan Province in China — but they have their own irrefutable reality.

"There's been an argument in the recent archeological literature that genetics gives a false picture of domestication as a rapid, geographically localized process," comments Kenneth M. Olsen, PhD, assistant professor of biology in Arts & Sciences at Washington University. "They argue instead that domestication likely involved much trial and error in many different geographic regions over a long period of time."

In a review of the genetics of plant domestication published in the advance online edition of *Trends in Plant Science*, Olsen, who uses genetic approaches to study the domestication of rice, cassava and coconut, and Briana L. Gross, PhD, a postdoctoral research scholar in his lab, review the recent genetic data and argue that genetic evidence doesn't conflict with the archeological evidence that domestication was gradual, dispersed and tentative.

The Domestication Syndrome

Plant domestication can be thought of as a two-step process. In the first step, plants acquire traits in what is called the "domestication syndrome" that make the plant worth the labor of cultivation. These include traits that allow a crop to be reliably sown, cultivated and harvested, such as

uniform seed germination and fruit ripening.

In the second step, the now domesticated plant is selected for improved qualities. It is in this stage, for example, that farmers might breed many different varieties of a crop that differ in grain taste, fruit color or fruit shape.

In the case of grains two of the most important traits in the domestication syndrome are the loss of shattering, and the loss of seed dormancy.

Shattering, or the tendency of seeds to break off the central grain stalk once mature, is an advantage for wild grains, because it helps to ensure the seeds disperse. But a crop plant must retain its seeds long enough that the seed heads can be gathered at harvest.



Red rice (shown above) is a red-seeded weed that infests cultivated rice fields in the United States. Genetic studies had suggested the weed might be a reversion of a modern domesticated rice to a feral form, in part because the red grain was known to spontaneously appear in crop fields. Gross, Olsen and their colleagues have just published results in the online edition of *Molecular Ecology* that show red rice is not a reversion but instead an invasive rice that was never cultivated in the United States. Credit: Kenneth M. Olsen

The shattering trait provides a good example of the apparent conflict between the genetic and archeological data. Artificial domestication experiments show that it is possible to breed nonshattering cereals quite quickly. But Old World archeological data indicates that nonshattering cereals appeared only gradually, and typically only after the emergence of another domestic trait: larger grain size.

The increase in grain size suggests the plant was already under cultivation, and that the seeds were being sown, or buried, rather than blown about on the surface. Why would the nonshattering trait emerge later than larger grain size?

"The answer, at least in some cases," Olsen suggests, "is that a mutation that led to a complete loss of shattering might make harvesting easier but it would also make threshing much harder." So the nonshattering trait might have lagged behind other domestic traits because it required an optimal combination of mutations that balanced seed retention for both harvesting and threshing.

"This is why rice is still somewhat shattering, unlike maize," Olsen says. "If you have complete loss of shattering it makes threshing very difficult; so it's a compromise."

A second trait in the domestication syndrome is loss of seed dormancy. A wild plant all of whose seeds sprouted at the first shower or warm spell would risk disaster, so most wild species hedge their bets and stagger the germination of seeds. But in the more controlled agricultural environment, where the seeds are sown all at once and reaped all at once, there is strong selection against seeds with this trait.

However, in this case too, it is possible to overshoot the mark. "In rice, if you completely select against dormancy you can get a phenomenon called pre-harvest sprouting, where grains germinate while they're still

on the stalk," Olsen says. "That's another case where selection has gone too far, and you're losing crop productivity."

More than one way to make a domestic plant

Any plant breeder can tell the difference between a weed and a crop plant, but figuring out the genetic differences between them is much harder. Searching for the relevant changes among all the genetic variation in a species is like groping in a fog, because most of the variation is neutral and not linked to significant variation in the plant's phenotype.

Quantitative Trait Locus (QTL) mapping is a statistical method that looks for strong associations between particular phenotypic traits and short DNA sequences that identify, or mark, particular locations in the genome. It is particularly useful for studying the inheritance of complex traits that are influenced by many genes and their interactions with the environment.

The main goal of QTL mapping is to understand whether a trait is controlled by a few genes of large effect or many genes of small effect. The assumption is that phenotypes under simple genetic control could be domesticated more easily than those whose traits had a complex genetic basis.

The genetic data indicate that important domestication traits are under simple genetic control but also, as Gross and Olsen write, that there are "many ways to make a domesticated plant." For example, genetic analysis shows that barley, common beans and Asian rice were domesticated more than once, a remarkable finding because the archeological evidence on this question is inconclusive.

QTL maps have also revealed that the same traits are sometimes

controlled by different constellations of genes. For example, different genes prevent shattering in the two domesticated lineages of barley.



Domestication is a two-step process; during the second step "improved" qualities are selected in the crop plant. One example Olsen has studied is the selection of glutinous varieties of rice, called sticky rice, which was actually selection for a mutation in a gene called Waxy. Mochi, shown above, are Japanese rice cakes made by pounding the sticky rice into paste and molding the paste into shapes. Credit: Cindy Ellen Russell for the Honolulu Star-Bulletin

Although QTL mapping has led to many insights about the domestication of plants, Gross and Olsen emphasize that genes cannot tell us everything. Trying to read the history of domestication out of the genomes of existing crop [plants](#) is like trying to read a book with many missing pages.

There's a simple reason for this. Living crops cannot provide information about any plant lineage that did not ultimately contribute to

a modern crop. So the genetic record is silent about domestication experiments that ultimately failed or were abandoned. If these experiments left a record, they left it only in archaeobotanical remains — which is what makes it difficult to reconcile that record with the genetic data.

Sticky rice, fragrant rice and other fun stuff

The second step in plant [domestication](#) is the fun one. Once a plant has become amenable to sowing and reaping, farmers set to work to improve it or diversify it.

One such improvement is sticky rice, a type of short-grained, famously glutinous Asian rice. Olsen, who has studied the origins of sticky rice, says that usually "about 20 percent of the starch in the rice is amylose and the rest is another starch called amylopectin. Amylose is an unbranched molecule and amylopectin is branchy; because it is branchy, the rice starch sticks to itself when it is cooked."

"In certain areas of the world, particularly Southeast Asia, people favored varieties of rice that were sticky," Olsen says. "By selecting sticky rice, they were actually selecting rice that had a mutation in a gene called Waxy. The gene mutation prevented the plant from making a protein responsible for a key step in producing amylose. When amylose was absent, the grains were filled with the stickier starch amylopectin."

The fragrance of cooking basmati or jasmine rice is another example of an improvement. What you smell when the steam wafts above the rice cooker is an aromatic compound called 2-acetyl-1-pyrroline (or 2AP), which is also an important note in the aroma cooked popcorn, bread crust, crabmeat -- and screwpine leaves. Screwpine leaves are aromatic leaves used to flavor rice dishes and sweets in India and southeast Asia.

The rice BADH2 gene underlies variation in the production of 2AP and a survey of this gene in aromatic rices around the world has shown that although one gene variant (or allele) is by far the most common, the aroma can be generated by a variety of mutations of the BADH2 gene.

Provided by Washington University in St. Louis

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