Do long-lived crops differ from annual crops in their genetic response to human domestication?

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Pecan (*Carya illinoinensis*) growing in the Missouri River floodplains near Hermann, Missouri. Pecan is one of the few native North American species which has entered the domestication process. Credit: Image courtesy of Allison Miller, Saint Louis University.

Most of what we have come to think of as our daily fruits, vegetables, and grains were domesticated from wild ancestors. Over hundreds and thousands of years, humans have selected and bred plants for traits that benefit us -- traits such as bigger, juicier, and easier-to-harvest fruits, stems, tubers, or flowers. For short-lived, or annual, plants, it is relatively

easy to envision how such human-induced selection rapidly led to changes in morphology and genetics such that these plants soon become quite different from their wild progenitors.

But what about longer-lived, perennial crops, such as fruit or nut trees? How do these long-lived species respond to short-term selection processes, and will this information be helpful in predicting responses to rapid climate changes?

Dr. Allison Miller (Saint Louis University, MO) and Dr. Briana Gross (National Center for Genetic Resource Preservation, USDA-ARS, Fort Collins, CO) are interested in the diversity of plant genomes in domesticated crops and the evolution of their breeding systems under domestication. They undertook an extensive review of perennials, primarily long-lived tree crops, comparing their morphology and genetics in response to human selection pressures to that of natural tree populations and annual crops, which is something we know a lot about. They published their findings in the September issue of the American Journal of Botany.

"Since their origins roughly 10,000,000 years ago, agricultural societies have been based primarily on annual grains and legumes such as corn, wheat, rice, common beans, and lentils," notes Miller. "The importance of these crops is without question; however, every agricultural society has also domesticated perennial plants and these are less well-known than the annuals."

In their article, Miller and Gross point out that one of the challenges to domesticating long-lived species is that they have especially long juvenile phases. This imposes limits on farmers because they have to wait years before they can evaluate, select, and cultivate fruits, in contrast to annuals that can be grown from seed every year. Moreover, like many trees in nature, perennial tree crops are often obligate

outcrossers, requiring pollination from another individual. Farmers have gotten around these "obstacles" by clonally propagating individuals with desirable traits.

While clonal propagation may seem like it would result in lower genetic variation, the authors observe that clonal propagation and a long juvenile phase means perennial tree-crops have actually gone through fewer sexual cycles since domestication and thus have remained closer, genetically, to their wild progenitors. Indeed, perennial fruit crops retain an average of 95% of the (neutral) genetic variation found in their wild counterparts, compared with annual fruit crops which retain about 60%.

Interspecific hybridization is very common in tree species in nature, and this ability to readily hybridize is an important trait in domestication -- once a hybrid is formed, it can become the basis for an entire new variety through clonal propagation. Thus, clonal reproduction can also result in rapid rates of change in domesticated systems because individuals with desirable traits can be reproduced exactly and extensively.

"The evolution of perennial plants under human influences results in significant changes in reproductive biology," notes Miller, "and in many cases, perennial crops have reduced fertility in cultivation."

While many annual crops were domesticated from self-compatible wild ancestors, few perennial crops were derived from selfing wild populations. Thus, domesticated perennials often encounter mate limitation barriers when one or just a few clones are planted across a geographic region. However, plants in these agricultural systems have responded by evolving alternative strategies to ensure fruit production. For example, grapes have shifted from having unisexual to bisexual flowers and to having self-compatible fertilization.

Genetic bottlenecks in cultivated populations occur when only a subset of wild individuals are brought under cultivation -- over time, the genetic base narrows as superior individuals are selectively propagated, resulting in elite cultivars that can be genetically depauperate. However, the authors found that many domesticated tree crops are derived from multiple areas, where seeds and cuttings were removed from geographically distinct wild populations. Moreover, many perennial species are highly heterozygous and clonal propagation maintains this heterozygosity at the individual level. Thus, perennial tree crops tend to have a much broader genetic bottleneck than annuals.

In light of the growing concern over monocultures and the loss of genetic diversity in our domesticated crops, Miller and Gross' review of perennial long-lived crops highlights the importance of maintaining long-lived perennials which may have lower environmental impacts as well as higher genetic variability within their populations.

"Understanding how basic evolutionary processes associated with agriculture (e.g., domestication bottlenecks, selective cultivation) impact plant species is critical for crop breeding and for the conservation of crop genetic resources," concludes Miller.

Scientists are also interested in how climate change might impact agriculture. In this framework, Miller is interested in exploring how perennial crops withstand heterogeneous climates over multiple years. "Little is known about the genomic basis of adaptation to climate in perennial plants, or how gene expression patterns may vary from year to year based on climatic conditions in a given location," she notes.

More information: Allison J. Miller and Briana L. Gross. (2011). From forest to field: Perennial fruit crop domestication. American Journal of Botany 98(9): 1389-1414. DOI: 10.3732/ajb.1000522

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