

DOMESTICATION

Polyploidy boosts domestication

A detailed phylogenetic study now shows that there is a compelling association between polyploidy and domestication, and that polyploidy more frequently occurs before domestication.

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Polyploidy and domestication are both important phenomena in plant evolution. Many important crops are polyploid, including banana, canola, cotton, oat, potato, sugar cane, sweet potato and wheat. A debate regarding a possible correlation between polyploidy and domestication in plants has continued for several decades. Now reporting in *Nature Plants*, Salman-Minkov and colleagues¹ have used statistical and computational approaches to examine the association between polyploidy and domestication based on a comprehensive data set. They concluded that domesticated plants have undergone more polyploidy events than their wild relatives, and that polyploidy more frequently occurred before domestication (Fig. 1).

Polyploid plants have multiple chromosome sets (derived from the same species or related species) due to abnormal cell division or through hybridization. Because of the increase in genome size and thus genetic diversity, polyploids can carry more favourable genetic variants compared to their wild diploid relatives — disease resistance and adaptation to diverse environments, or increased adaptation to the current local environment². Polyploidy increases the amount of raw material on which natural and artificial selection can act, leading to increased adaptation to the local environment due to novel variants in the polyploids or fixed heterozygosity. Genetic diversity can be greatly reduced during a domestication bottleneck — so the additional genetic diversity provided by polyploidization can be crucial. In addition, many genomic, transcriptomic and epigenetic novelties are generated through polyploidy³. Polyploidization also alters dominance relationships among alleles; it is harder to select and fix recessive mutations. Dominance can preserve function if any of several copies of an allele remain. Polyploidization of a domesticate can also create genetic isolation from a wild progenitor, effectively limiting gene flow between wild and domesticated plants so that favourable traits can be maintained in

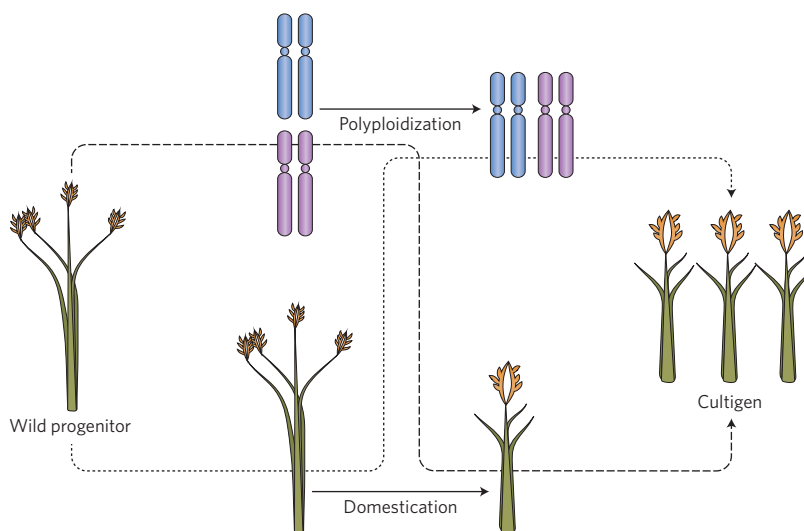


Figure 1 | Two possible scenarios involving polyploidy and domestication. Polyploidy could precede domestication (dashed line), or domestication could come first (dotted line).

the cultivated crops during domestication^{4,5}. Some polyploids exhibit 'gigantism' for traits that can mimic those observed in the domestication syndrome, such as increased seed or grain size. Polyploids may therefore be more frequently the target of human efforts at domestication owing to increased 'curb appeal'.

However, in a few previous investigations, little correlation was found between polyploidy and domestication^{5,6}. Although polyploidization can confer fitness advantages, favourable new mutations are more quickly fixed and the fitness effect of these mutations can be more easily identified in diploid species than polyploid species. Therefore, it seemed reasonable that there is little association between polyploidy and domestication, because polyploidy is not exclusively advantageous relative to diploidy in plant evolution.

Salman-Minkov and colleagues assembled a large data set with improved phylogenetic comparative methods and a more current definition of polyploidy. Early studies (such as ref. 6) used a chromosome number threshold (11 or 13, in their

case). Due to genome downsizing, using chromosome number to define polyploids is problematic. Salman-Minkov and colleagues reconstructed the phylogeny of each genus using publicly available sequence data. The polyploidy events were inferred based on shifts in chromosome numbers along the phylogeny. Ploidy shifts were mapped onto the phylogenetic tree using a probabilistic model of chromosome number evolution. Using this approach, the authors find a compelling association between polyploidy and plant domestication.

They also showed that polyploidy more frequently occurs before domestication. Based on its advantages, polyploidy preceding domestication sounds intuitively more reasonable than domestication followed by polyploidy. Higher genetic diversity with more adaptive genetic variants in polyploids could benefit the domestication process. However, disentangling the order of polyploidy and domestication is challenging (Fig. 1). There are also studies in support of the 'domestication followed by polyploidy' scenario; it was found that human activities


resulted in artificial sympatry, hybridization and polyploids in backyard gardens⁷. Salman-Minkov and colleagues thoroughly investigated this issue based on a much larger data set, and showed that polyploidy followed by domestication is more likely (Fig. 1).

Despite the significant association between polyploidy and plant domestication, as well as the finding that polyploidy usually occurs before domestication, there are several notable exceptions. The polyploidization of wheat, for example, was due to human cultivation after domestication⁸. Polyploidy in wheat resulted in the emergence of the free-threshing grain trait and increased the diversity in wheat grains, such as grain hardness or softness³.

This study demonstrates the important role played by polyploidy in plant evolution, but polyploid crops have received less research attention than their diploid relatives since the advent of molecular markers. This could be because in polyploid genomes, multiple paralogues (copies of a gene) are found at each locus. A diploid organism with two alleles at a locus can have one of three possible genotypes — but a tetraploid species can have genotypes AAAB, AABB, and so on, all of which carry different dosages of the same two alleles. While resequencing could potentially distinguish

all possible alleles at a locus, this would have been, until recently, a very involved task that required a great deal of effort to distinguish polymorphisms within homologous portions of the genome from divergence between progenitor species⁹. Short-read sequencing technologies have the advantage of creating reads from a single molecule and thus a unique sample of a polyploid genome, but can be difficult to map back to a unique location in the reference genome¹⁰. Because polyploidy creates at least a rough doubling of genome size, twice as much sequence is needed to achieve the same level of coverage as in a diploid relative. This has been an issue for comparative resequencing studies, single-nucleotide polymorphism discovery, and for reference genome assembly. Emerging long-read sequencing technologies hold great promise for the study of polyploid species because they can potentially create sequence reads of sufficient length to distinguish sequences contributed by each of the chromosomes in a polyploid genome.

The current study also has some limitations, such as the relatively low resolution of the phylogenetic placement. More precise timing of domestication events could provide deeper insight on this important topic. Nonetheless, the authors provide strong evidence for the importance

of polyploidy in plant domestication. Polyploidization increases genetic diversity, fosters adaptation to new environments, introduces new genetic combinations, and can create heterotic effects. Polyploidy accelerates domestication and the process of selecting favourable new traits. As all these areas are challenges currently facing crop breeding, polyploidy formation should be considered as an important potential path to future crop improvement. 

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