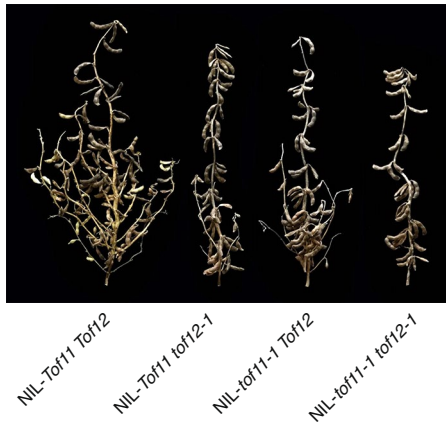


## SOYBEAN DOMESTICATION

## Stepwise phenological adaptation

Nat. Genet. <http://doi.org/dqx8> (2020).



Credit: Image courtesy of Fanjiang Kong

Initially domesticated in the temperate regions of China, cultivated soybean expanded its geographical distribution toward the north by shifting to an early flowering and maturity habit. Although a number of genetic variants have been found to account for the variations of flowering time in soybean, the genes facilitating this change for early latitudinal adaptation remains unknown. Sijia Lu, from Guangzhou University, and colleagues now report two homologous *pseudo-response regulator* (*PRR*) genes, *Tof12* and *Tof11*, that sequentially contributed to high-latitude adaptation during early soybean domestication.

Using a panel consisting of 424 newly resequenced accessions and another panel of 809 previously re-sequenced accessions, as well as a bi-parental population, the researchers detected loci associated with flowering times by association and linkage mapping. Two loci located in chromosomes 11 and 12, referred to as *Tof11* and *Tof12*, were detected in all three populations and further narrowed down to two *PRR* genes. Their roles in controlling flowering time were validated by transgenic complementation.

Genetic analyses support that *Tof11* and *Tof12* function independently with some redundancy, and their function depends on the legume-specific *E1* gene. *E1* represses two key *FLOWERING LOCUS T* (*FT*) homologues, *FT2a* and *FT5a*, and thereby suppresses flowering under long day conditions. *E1* gene is repressed by *LATE ELONGATED HYPOCOTYL* (*LHY*) genes which can be repressed by *Tof11* and *Tof12*. So *Tof11* and *Tof12* overexpression increases *E1* expression and consequently represses the expression of the *FT* homologues, while the loss-of-function mutations, *tof11* and *tof12*, derepress *FT2a* and *FT5a*, leading to early flowering. Figure 1 shows four near-isogenic lines (NILs) with different *Tof11/tof11* and *Tof12/tof12* genotypes and their corresponding flowering and maturity phenotypes.

A very strong selection signature was detected around the *Tof12* gene, with a loss-of-function *tof12* mutation strongly favoured in landraces and fixed in all improved cultivars. Loss-of-function *tof11* have arisen multiple times, but only one mutation that occurred in the background of the *tof12* mutation becomes widespread in domesticated soybean. Molecular dating suggests that this *tof11* mutation occurred 2,500 years after the *tof12* mutation, so they were sequentially incorporated into the cultivated soybean gene pool, conferring an additive early flowering phenology.

The *tof12* mutation experienced artificial selection in a strength similar to that experienced by other well-known soybean domestication genes regulating seed dormancy and shattering, suggesting these phenotypes may have been selected in parallel. The allele frequency patterns of the three genes, *Tof12*, *Tof11* and *E1*, indicated they were sequentially adopted in breeding for high-latitude adaptation.

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Published online: 9 April 2020  
<https://doi.org/10.1038/s41477-020-0644-0>