MAIZE GENETICS

Valuable allele in the wild

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Credit: Image courtesy of Feng Tian

Upright architecture with a small leaf angle represents an elite trait in maize that enables dense planting and yield increase. Although previous mutant analysis has uncovered two genes, *lg1* and *lg2*, that control leaf angle, their mutant alleles cause phenotypes that are too severe to be useful in maize production. To understand the natural variations that regulate maize leaf angle, Jingjie Tian and Chenglong Wang, from China Agricultural University, and colleagues cloned the causal genes underlying two quantitative trait loci (QTLs), *UPRIGHT PLANT ARCHITECTURE 1* (*UPA1*) and *UPA2*, that confer upright architecture in maize.

The researchers used a segregating population derived from a cross between a maize inbred line and a teosinte accession. Among the 12 found QTLs, *UPA1* and *UPA2* displayed the largest phenotypic effects and were chosen for positional cloning.

UPA2 was mapped to a 240-base pair non-coding region 9.5 kb upstream of a B3-domain transcription factor gene, *ZmRAVL1*, and is a *cis*-element that regulates the expression of *ZmRAVL1*. The teosinte *UPA2* allele confers a smaller leaf angle and is conducive to dense planting. Consistently, *ZmRAVL1* positively regulates leaf angle, as disrupting this gene reduces leaf angle, while overexpressing this gene increases leaf angle. The causal variant of *UPA2* was found to be a two-base sequence polymorphism that affects the binding of the DROOPING LEAF 1 (*DRL1*) protein. *DRL1*

interacts with the *LIGULELESS 1* (*LG1*) protein, which binds to the promoter of *ZmRAVL1* and activates its expression. So, the teosinte *UPA2* allele indirectly regulates *ZmRAVL1* expression via the *DRL1*–*LG1*–*ZmRAVL1* module, which explains how the two-base causal variant regulates the expression of downstream *ZmRAVL1*.

The other QTL, *UPA1*, was mapped to a *brassinosteroid C-6 oxidase* (*brd1*) that converts 6-deoxocastasterone to castasterone, the immediate precursor of the hormone brassinolide. Unlike *UPA2*, the teosinte *UPA1* allele confers a larger leaf angle. Mutant and transgenic analyses validated the function of *brd1* in regulating maize leaf angle. Genetic and biochemical evidences suggest that the *ZmRAVL1* protein binds to the promoter of *brd1*, activates *brd1* transcription and positively regulates castasterone levels. So, *UPA2*–*ZmRAVL1* modulates leaf angle by regulating *brd1* and endogenous brassinosteroid content.

Although the teosinte *UPA2* allele is present only in a minor proportion of teosinte accessions and was lost during maize domestication, field trials have shown that introducing this rare allele or a CRISPR-edited *ZmRAVL1* allele into inbred or hybrid maize reduces leaf angle and enables dense planting as well as yield increase.

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