

# Exploring the maize of genetic variation

Understanding the basis of genetic variation for desirable agronomic traits in the staple food source *Zea mays* (maize) is important for crop improvement and for developing maize as a model for complex traits. Two new studies describe the construction and potential applications of a new resource for mapping quantitative traits in maize, illustrating that it can be used for dissecting the genetic architecture of important traits, such as flowering time.

Two approaches are commonly applied for detecting quantitative trait loci (QTLs) — linkage mapping and association mapping — but both have limitations, such as the low resolution of linkage mapping and the low power of association mapping for detecting rare alleles. Buckler, Holland, Kresovich, McMullen and colleagues combined the advantages

of both approaches by devising a nested association mapping (NAM) approach. They derived the NAM resource by crossing a common reference maize strain with 25 diverse lines to maximize the allelic diversity captured by NAM, and this process produced ~5,000 recombinant inbred lines (RILs). The NAM population can be used to detect QTLs by performing linkage mapping using a moderate number of markers, followed by high-resolution association mapping using a high-density marker map. Because the individuals in a particular RIL are almost genetically identical, the phenotype of a given quantitative trait can be scored in multiple individuals with the same genotype in multiple environments, which increases the power of identifying QTLs.

To enable mapping studies and to explore recombination patterns in these lines, the authors created a composite genetic map with an average marker density of 1 SNP per 1.3 cM. By comparing the recombination events in the RILs, they found extensive variation in the recombination frequency across the 25 maize families that constitute the NAM population. Interestingly, the high levels of heterozygosity that were observed near the centromeres suggest a possible explanation for the phenomenon of heterosis, in which crossing two inbred lines improves the fitness of the offspring — the DNA near the centromeres might not be reshuffled as efficiently as the

DNA in the rest of the chromosome during inbred development.

In a second paper, Buckler *et al.* used the NAM resource to study the genetic variation in flowering time. They analysed ~1 million plants in 8 environments and concluded that differences in flowering time are caused by the cumulative effects of many small-effect QTLs, with few epistatic or environmental effects. These observations are consistent with QTL analyses in other organisms, such as mice, flies and humans. However, the results contrast with the genetic architecture of flowering time in other plants, such as rice, barley and *Arabidopsis thaliana*, in which QTLs with large effects account for most of the variation in flowering time and epistatic effects and environmental interactions also have a role.

The NAM resource is expected to be an important genetic tool, although the parent strains will need to be sequenced and their genetic polymorphisms will need to be projected onto the NAM lines before the resource can be most efficiently used for high-resolution trait mapping in maize.

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**ORIGINAL RESEARCH PAPERS** McMullen, M. D. *et al.* Genetic properties of the maize nested association mapping population. *Science* **325**, 737–740 (2009) | Buckler, E. S. *et al.* The genetic architecture of maize flowering time. *Science* **325**, 714–718 (2009)  
**FURTHER READING** Mackay, T. F. C. *et al.* The genetics of quantitative traits: challenges and prospects. *Nature Rev. Genet.* **10**, 565–577 (2009)



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