

Adaptive variation in wild relatives of modern maize has potential use in breeding

We present a high-resolution genomic variation map that greatly expands the sequence information for maize and its wild relatives in the *Zea* genus. Population genetics of *Zea* spp. provide a vast trove of adaptive alleles that are absent in maize, with the potential for accelerating future breeding by reintroducing genetic diversity.

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The problem

Climate change affects crop production, further exacerbating the gap between inadequate food supplies and growing human populations¹. New varieties of crops with both increased yield and improved adaptation to diverse environments are urgently needed². Maize (*Zea mays*) is widely grown worldwide, but has lost abundant genetic diversity for adaptation owing to population bottlenecks (certain events that can strongly reduce the size of a population) during domestication and breeding³. Teosintes (wild congeners of maize) are adapted to a diverse range of environments, from hot, humid, subtropical regions to cold, dry and high elevations. They exhibit biotic and abiotic adaptations (such as resistance to extreme environments and disease) that are absent in modern maize, and provide a wealth of genetic diversity that could be used in modern breeding⁴. However, the potential of teosintes as sources of useful diversity in maize remains poorly understood⁵.

The discovery

To construct a diversity map of *Zea* spp., we sequenced 237 teosinte accessions (which are samples of a plant species – including *Z. nicaraguensis*, *Z. luxurians*, *Z. perennis*, *Z. diploperennis*, *Z. mays* subspecies (ssp.) *huehuetenangensis*, *Z. mays* ssp. *mexicana* and *Z. mays* ssp. *parviglumis* – collected from a specific area), encompassing all described species and subspecies in the *Zea* genus, and combined these data with genome sequencing data from 507 cultivated inbred maize lines that represent both temperate and tropical regions. We also reconstructed the evolutionary histories of divergence times, population sizes and relationships among taxa, creating the most complete genus-wide phylogeny so far. To explore genetic diversity, we profiled the diversity of single-nucleotide polymorphisms (SNPs), small sequence motifs (*k*-mers), transposable elements and inversion polymorphisms across all *Zea* taxa. Furthermore, to identify adaptation alleles from teosintes with potential for modern breeding, we searched for selection signals (changes in genetic differentiation among populations due to adaptation that result in increased frequency of favorable alleles) in different *Zea* taxa.

We identified over 70 million SNPs and nearly 9 million insertions or deletions (indels). Phylogenetic analysis estimated that the *Zea* genus split from its sister genus *Tripsacum* only around 650,000 years ago. Divergence among *Z. mays*, *Z. luxurians* and

Z. diploperennis was nearly contemporaneous, occurring roughly 120,000 years ago (Fig. 1a). Nucleotide diversity is higher in teosinte taxa than in the much larger panel of maize lines, and genetic differentiation (estimated by the fixation index, F_{ST}) between teosinte taxa is often lower than that found between inbred maize and teosintes (Fig. 1b), consistent with the historical reduction of diversity that occurred during domestication and breeding. Around 24% of the SNPs and 20% of the indels identified across all taxa are unique to individual taxa, with many more found in teosintes than in maize.

We further conducted a genome-wide search for signals of selection to identify putatively adaptive alleles in teosintes that could be used in modern breeding. In addition to this broad search, we focused on local adaptation in highland teosinte and high-latitude maize, and found the key role of pathways involved in flowering time in their adaptation (Fig. 1c). In particular, we validated the circadian clock gene *PRR7*, which showed convergent patterns of selection in maize and teosintes, and the maize-specific candidate gene *COL9*, which is involved in the photoperiod pathway.

The implications

Our research demonstrates the utility of looking to locally adapted teosintes to find genetic diversity relevant for maize breeding. Our initial analyses identified hundreds of potential candidate genes that could be further investigated in future breeding.

We found that most of the selection signals occurred in intergenic regions of the genome, which suggests that other ‘-omic’ scale analyses will be necessary to identify the mechanisms and roles of these loci. In addition, further analyses are necessary to determine the function of candidate adaptive genes and how they respond to different environmental factors.

Our next steps are to generate multi-omics data under different environments. In combination with genome-editing tools, we want to explore the evolution trajectories of regulatory networks in *Zea* spp. during their adaptation to different environments, interrogate the potential function of noncoding regions targeted by selection, and determine whether these adaptive genes can be used for accelerating modern maize improvements.

Lu Chen and Jianbing Yan

National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan, China.

EXPERT OPINION

“The study has generated an impressive, vast collection of genomic teosinte data. The genomic and allelic repertoire of teosintes and the genus history are of particular broad interest and importance, owing to the domestication origin of maize from teosintes and the region where

the different species originate from. Thus, genes or alleles that might have been lost during domestication may well provide an important allelic repertoire for new breeding routes.”

Klaus F. X. Mayer, Helmholtz Center Munich, Neuherberg, Germany.

FIGURE

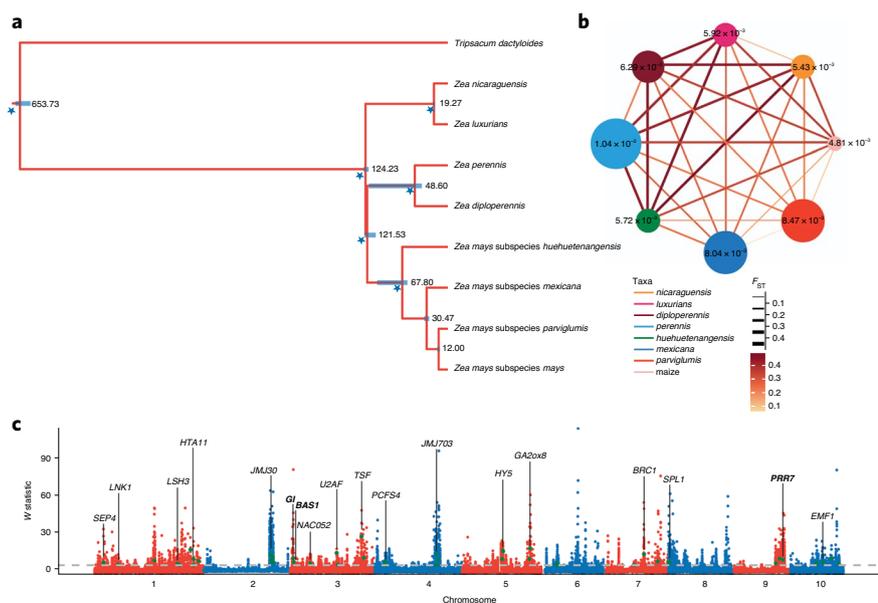


Fig. 1 | Evolution and local adaptation of *Zea* genus. **a**, Estimated divergence times (in thousands of years before present). Blue bars indicate the 95% highest posterior density intervals (confidence level). Stars indicate nodes with posterior probability (probability of species placement) of 1. **b**, The values in the nodes are the mean nucleotide diversity in each taxon; the width and color of the edges represent F_{ST} values between taxa. **c**, Genome-wide selection signals (W statistic reflecting smoothed XP-CLR score) between *Z. mays* ssp. *mexicana* and *Z. mays* ssp. *parviglumis*. The horizontal gray dashed line represents the top 5% cutoff. Genes associated with flowering time are marked with green points; bold font indicates convergent adaptation genes. © 2022, Chen, L. et al.

BEHIND THE PAPER

Our groups focus on maize genetics and molecular breeding. In recent decades, increasingly frequent weather disasters have caused a severe reduction of crops. In particular, floods ruined all the crops that we planted in the summer of 2016 in Wuhan, China. To cultivate maize that can adapt to future climate change, we have tried to find clues from teosintes, which can adapt to diverse environments. While we were investigating the extent of divergence between teosinte and

maize and the local adaptation of teosinte, we met Jeffrey Ross-Ibarra, and our collaboration started. The hardest challenge was collecting enough samples to represent these taxa from our reliable partners during the COVID-19 pandemic. We would like to sincerely thank our colleagues all over the world for their support and help in sharing materials. We look forward to sharing our data in return, and providing them with valuable information. **L.C. and J.Y.**

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FROM THE EDITOR

“This study stands out because of the well-designed sampling of teosinte accessions and the high-density genomic variation map of maize and all wild taxa in the *Zea* genus. It not only provides a genus-wide resource of genetic diversity, but also expands the understanding of convergent adaptation in *Zea* spp. and the potential use of adaptive variants for maize improvement.”
Wei Li, Senior Editor, Nature Genetics.