

The Maize Genome

The Domestication of Maize



Corn, also known as maize (from the Spanish *maíz*), was first domesticated nearly 10,000 years ago from teosinte, a wild grass that looked quite different from our modern crop. Teosinte grew in Mexico and Central America as a bushy plant with many spikes, the precursor to our familiar ear of corn. The small teosinte spikes had only two rows of nearly inedible kernels, or seeds, each enclosed by a hard covering. These seeds separated individually at maturity and were dispersed widely. In probably less than a thousand years, the tiny spikes of ancestral teosinte transformed into larger ears with edible kernels that remained on the cob for easy harvest. How these dramatic changes occurred has been a puzzle for over a century. Geneticists are now convinced that humans living in the Balsas River region of Mexico were foraging teosinte seeds when they noticed rare aberrations—likely caused by random mutations—that increased spike size dramatically. Seeds were propagated from these bigger spikes, and thus the remarkable events of domestication began. By studying the maize genome, researchers have now confirmed that mutations in single genes, such as *Teosinte glume architecture1* (*Tga1*), alter kernel and plant structure and that changes in many genes influence complex developmental traits, such as the time to flowering. As human populations migrated throughout the Americas, new varieties of maize were selected to grow in local environments. Some varieties were maintained as so-called landraces, each growing in ecological niches in Mexico and South America. Now, these varieties and landraces hold a wealth of genetic diversity, which is being tapped for both basic research and as traits for crop breeding.



Zea mays ssp. parviglumis, descendent from the original teosinte, shown here growing in Ames, IA (Image: David Cavagnaro, Decatur, IA).



The cradle of maize domestication was in the Balsas River basin, marked with pin (Image: Shutterstock.com/KathBinn).



Diverse ears of corn can be seen at a market in Pisco, Peru (far left; Image: Candice Gardner, USDA/ARS). A statue of an Aztec maize deity (left), holding corn ears in hand, shows the significance of maize in the lives of Mesoamericans (Image: The Dolan DNA Learning Center, Cold Spring Harbor Laboratory).



The tiny spike of teosinte (left) gave rise to the large edible corn ear of today (right) (Image: Hugh Iltis).

Maize Genetics in the 20th Century



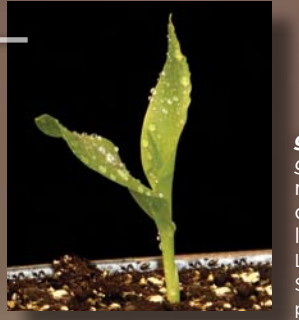
Maize geneticists at Cornell University in the early 1920s included (left to right) Charles R. Burnham, Marcus M. Rhoades, Rollins A. Emerson, Barbara McClintock, and (crouching) George W. Beadle. McClintock was awarded a Nobel Prize for her discovery of transposons in maize (Image: MaizeGDB and with permission of W. B. Provine).



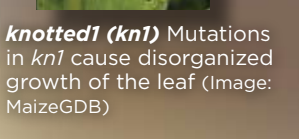
A genetic map from 1937 displays the 10 maize chromosomes. Mutants are used to map and study genes and develop traits for breeding maize as a commercial crop. Sample mutants and chromosomal positions are shown below. (Image: MaizeGDB).



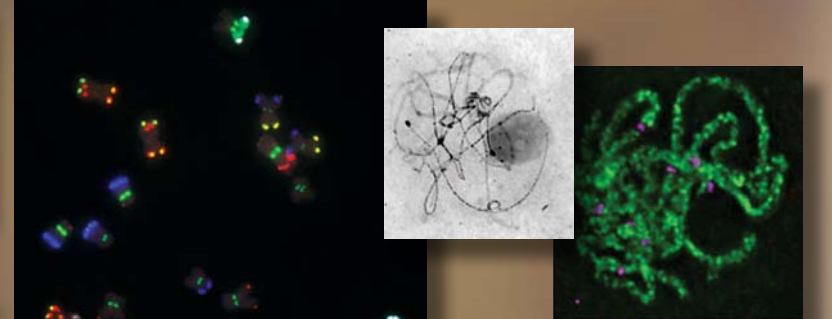
ramosa1 (*ra1*) Mutations in *ra1* cause extra branching in the ear early in development (Image: Erik Vollbrecht, Iowa State University, and Rob Martienssen, Cold Spring Harbor Laboratory).



glossy4 (*gl4*) Mutations in *gl4* affect waxes on juvenile maize leaves so that water droplets accumulate when the leaf is sprayed (Image: Sarahen Liu and Patrick S. Schnable, Iowa State University and reprinted by permission from the Genetics Society of America).



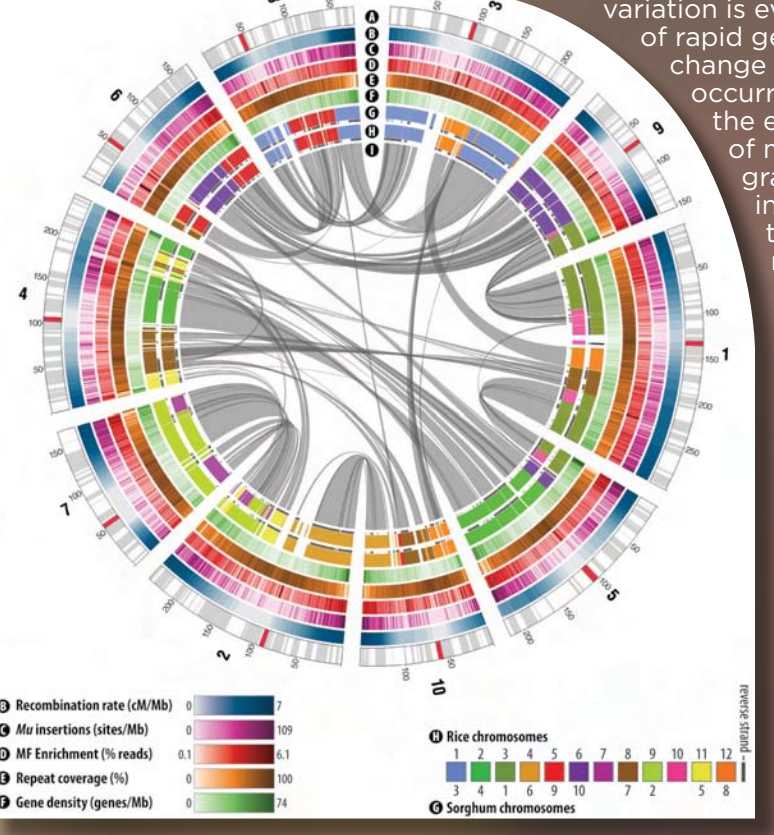
knotted1 (*knt1*) Mutations in *knt1* cause disorganized growth of the leaf (Image: MaizeGDB).



Maize meiotic chromosomes were first visualized by Barbara McClintock and others (upper middle; Image: Cold Spring Harbor Laboratory Research Archives). Similar meiotic stages can now be detected using antibodies to proteins associated with the DNA (upper right; Image: R. Kelly Dawe, University of Georgia) and fluorescently labeled DNA probes identify regions of interest in condensed somatic maize chromosomes (left; Image: Patrice S. Albert and James A. Birchler, University of Missouri).

The Dynamic Maize Genome

Maize has a strikingly dynamic genome: two maize varieties show as much DNA sequence variation as that observed between two different species. Also, genes present in one maize variety may be absent in another. Such variation is evidence of rapid genome change that occurred during the evolution of maize. The grass lineage that includes maize and teosinte diverged from rice and wheat approximately 50 million years ago. Subsequently, the full complement of chromosomes doubled in number in the ancestor of teosinte. Analysis of the sequenced genome of the Midwestern variety, B73, demonstrates that this ancestral duplicated genome underwent significant rearrangement, with pieces of chromosomes inverted, exchanged, transposed, further duplicated, or lost. Transposons contributed substantially to genome variation. Some classes of transposons cluster near centromeres, while others are found near genes that lack the chemical modification of methylation. Most, however, are located in heavily methylated, intergenic regions, contributing to the distinctive genome of each inbred variety. Comparative genomics studies are useful to identify genes in maize that are similar to those found in other plant species. Using these methods, study of the genome of the Mexican maize landrace, *Palomero toluqueño*, identified genes under selection homologous to those that are suspected to be involved in metal processing. Genome analysis demonstrates that landraces and worldwide varieties are highly diverse, making preservation of their unique molecular heritage important for cultural, scientific, and agricultural reasons.



Sequence analysis of the maize variety, B73, shows the dynamic nature of the maize genome. The outer rings are maize chromosomes (labeled 1 to 10) with duplicate regions connected by ribbons, showing the large related segments derived from each of the ancestral genomes (Image: From Schnable et al., *Science* 326 (5956) (2009); DOI: 10.1126/science.1178437).

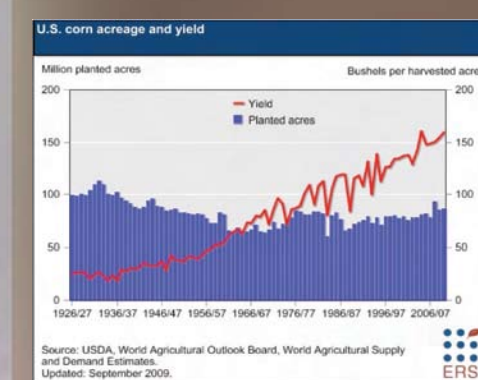
Maize Genomics Browsers and Genetics Resources
www.maizegdb.org
maizegenetics.org
magi.plantgenomics.iastate.edu
www.plantgdb.org
www.plantgdb.org/CoGe
www.phytozome.net/maize.php
www.ncbi.nlm.nih.gov/genomes/PLANTS/PlantList.html

Functional Genomics Resources
www.panzea.org
maize.jvri.org/cellgenomics/index.shtml
www.plantgdb.org/ra1/ActbTagging
uniformmu.uf-genome.org
mtm.cshl.org
maizecdna.org
genome.purdue.edu/maize/tiling
plantbio.berkeley.edu/~mukiller
plantcentromeres.org
maize-mapping.plantgenomics.iastate.edu

National and International Organizations
www.inpca.com
www.cimmyt.org

Background maize kernels: Purple-colored sectors and spots demonstrate the phenotypic effects of chromosome breakage caused by activity of transposable elements called *Activator* and *Dissociation*, in one of the earliest examples of transposition (Corn ear from McClintock collection grown in 1949, Cold Spring Harbor Laboratory. Image: Jim Duffy and Rob Martienssen, Cold Spring Harbor Laboratory).

From Gene Discovery to Application



Soon after the discovery of heterosis, corn yields began to increase steadily (Graph: ers.usda.gov).



A cross between two smaller inbred plants (left and right) produces more vigorous and productive hybrid offspring (center; Image: Jun Gao and Patrick S. Schnable, Iowa State University, reprinted by permission from Springer-Plant Sciences).



Improved hybrids, combined with advances in crop management, contributed to increased yields. (Scale bar = People standing to left of freshly harvested corn; Image: Patrick S. Schnable, Iowa State University).



The *opaque2* mutation was used by breeders in Africa and at CIMMYT (*Centro Internacional de Mejoramiento de Maíz y Trigo*) to develop lines, called Quality Protein Maize (left), with increased quantities of the amino acids lysine and tryptophan (Image: Brian A. Larkins, University of Arizona).



The *shrunken2* mutation causes a block in starch synthesis: sugar precursors accumulate in the milky fluid of the kernel, making sweeter tasting corn. The kernels deflate when the ear dries, as above (Image: William F. Tracy, University of Wisconsin-Madison).

The Future

Maize has adapted through domestication to nearly every climate across the globe, and many societies now depend on maize to feed expanding populations of people and livestock. Although breeders and agronomists have increased crop yields over the past century, the world's growing population strains global food production as climate patterns are disrupted, arable land diminishes, and nonrenewable energy supplies dwindle. Solutions will be made possible by global cooperation in which scientific and technological progress translates basic discoveries into practical applications. To this end, the genome sequences of maize and other crops are significantly enhancing established breeding efforts. Soon it will be possible to reconstruct and fully understand the genetic basis for maize growth and development; new tools will permit researchers to pinpoint functions and study interactions of gene products and plant metabolites with the environment. This basic information can be used to tailor maize varieties, through molecular breeding, to thrive in new environments, generate new products, and increase yields. Other advances include the use of transgenes that help maintain crop yields despite environmental pressures from drought, insects, pathogens and weeds. Maize also serves as a model grass to develop methods for optimizing plant-based biofuel production. The maize genome sequence thus enables researchers to make targeted improvements, allowing us to keep pace with a future as dynamic as the maize genome itself.



A farmer tends her crop. Maize can be modified to suit local environments and to satisfy cultural needs (Photo: Arjen van de Merwe).

Tools are being developed to take advantage of the maize genome and to meet the needs of the future. This is being accomplished through the use of new sequencing, proteomic, metabolomic and cellular level technologies. The sample below shows just a few of the functional genomics resources being developed.



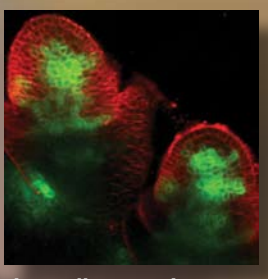
UniformMu: An inbred transposon population is used for functional genomics (Image: A. Mark Settles with Donald R. McCarthy, Karen E. Koch, L. Curtis Hannah, University of Florida).



mtmDB: Mutations, such as in *branched silkless1* (*bdl*) shown here, can be found using a transposon tagging resource (Image: Rob Martienssen, Cold Spring Harbor Laboratory).



Genome databases, such as the maize genomics and genomics databases, synthesize and make accessible large and increasingly complex datasets (Image: MaizeGDB).



Maize cell genomics: Fluorescent tags mark proteins in cells, allowing for functional studies (Image: From Mohanty et al. 2009. *Plant Physiology* 149:601-605. www.plantphysiol.org. Copyright: American Society of Plant Biologists).



Ds mutagenesis: A colored sector in the tassel represents *Ds* transposition, a tool for inducing new mutations (Image: Thomas P. Bruntell, Boyce Thompson Institute).



Panzea: Maize diversity is evident in a mapping population generated by crossing different varieties with B73, ultimately producing distinct lines that serve as the "raw material" for further maize improvement. Each row shows variation in one visible trait of plant height (Image: From McMullen et al., *Science* 325, 737 (2009); DOI: 10.1126/science.1174320).



Teosinte and Maize drawings by Hugh Iltis; from Doebley et al., *Proc. Natl. Acad. Sci. U.S.A.* 87, 9688 (1990).