

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 architecture 1 (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).

Teosinte



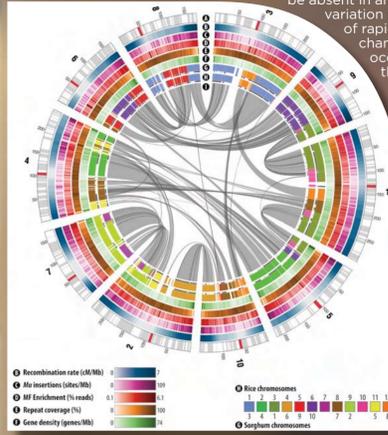
Diverse ears of corn can be seen at a market in Pisco, Peru (far left; Image: Candice Gardner, USA/ARS). A statue of an Aztec maize deity (left), holding corn ears in hand, shows the significance of maize in the lives of Mesoamericans (Image: The Dolan DNA Learning Center, Cold Spring Harbor Laboratory).



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

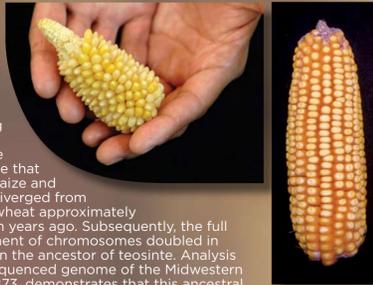
The Dynamic Maize Genome

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).

Two maize genomes sequenced recently were B73, an elite inbred line grown in the Midwestern United States (right; image: Ruth Swanson-Wagner and Patrick S. Schnable, Iowa State University, reprinted by permission from Springer-Plant Sciences), and *Palomero toluqueño*, a popcorn landrace grown in the highlands of Mexico (left; Image: Jaime Padilla, Irapuato, Guanajuato, Mexico).

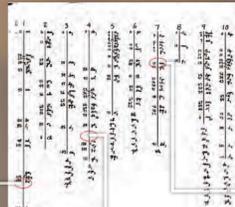


Maize Genetics in the 20th Century



Maize geneticists at Cornell University in the early 1920s included (left to right) Charles R. Burdham, 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).

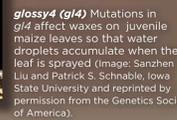
Maize emerged as a model research plant in the early 20th century partly because its domesticated traits were ideal for genetics experiments. Controlled genetic crosses were possible because the male tassel was separate from the female ear. Also, genes controlling seed and plant colors were ideal markers for studying patterns of inheritance. Geneticists developed methods to observe the distinctive meiotic chromosomes of maize, ushering in a new scientific discipline: cytogenetics. For the first time, researchers could study chromosome behavior and could associate genes with individual chromosomes using visible cytogenetic markers. The discovery of transposons—pieces of mobile DNA—revolutionized the field of genetics and demonstrated the dynamic nature of the maize genome. By the second half of the 20th century, maize geneticists had studied hundreds of mutants, mapped gene locations, cloned the first plant genes, and identified transposon-induced genome rearrangements among closely related maize varieties. Meanwhile, a physical map of the maize genome was populated with markers and was integrated with the maize genetic map. These tools, combined with gene expression profiles and other resources, provided the necessary foundation to sequence the maize genome.



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).



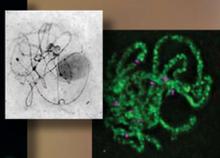
ramosal (ra1) Mutations in *ra1* cause extra branching in the ear early in development (Image: Erik Volkrecht, Iowa State University, and Rob Martienssen, Cold Spring Harbor Laboratory).



knotted1 (kn1) Mutations in *kn1* cause disorganized growth of the leaf (Image: MaizeGDB).



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).



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: Patricia S. Albert and James A. Birchler, University of Missouri).

Maize Genomics Browsers and Genetics Resources
www.maizegdb.org
maizegenetics.org
mgpl.plantgenomics.iastate.edu
www.grameire.org
www.plantgdb.org
synteny.cnr.berkeley.edu/CoGe
www.phytozome.net/maize.php
www.ncbi.nlm.nih.gov/genomes/PLANTS/PlantList.html
National and International Organizations
www.icas.org
www.cimmyt.org

Functional Genomics Resources
www.panzea.org
maize.jvri.org/cellgenomics/index.shtml
www.plantgdb.org/pa1/Actb5Tagging
uniformmu.uf-genome.org
mtm.cshl.org
maizecna.org
genome.purdue.edu/maizetilling
plantbio.berkeley.edu/~mkillier
plantcentromeres.org
maize-mapping.plantgenomics.iastate.edu

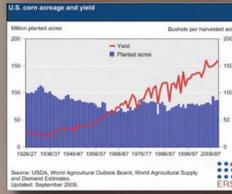
Maize Stock Center Seed and Resources
maizecoop.cropsci.uiuc.edu
www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl?Zea
public.iastate.edu/~usda-gem

Educational Resources on Maize
www.agry.purdue.edu/ext/corn/index.html
www.dnalc.org/resources/dnatoday
weedtowonder.org
www.extension.iastate.edu/hancock/info/corn.htm

Seed company resources are also available through individual company websites. Also see maizegdb.org/POPcorn for additional public resources.

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).

Early explorers of the Americas took maize back to Europe during the 16th century. Since then, maize has spread globally and is now a major world crop. Yields have increased steadily over the past century as maize became an important source of food, feed, fiber and, more recently, biofuels. During this period, scientists, breeders, growers, and seed companies worked together to translate basic research in maize genetics into practical applications. One event of particular impact was the demonstration of hybrid vigor, or heterosis, which results when two parental varieties, both showing reduced stature caused by inbreeding, are crossed to produce more robust hybrid offspring. Vigorous hybrids increase crop productivity dramatically and are now used for nearly all commercial corn production. Geneticists are still unraveling the underlying molecular basis of heterosis and the sequencing of maize genomes will provide new insights into its mechanisms. Genomics resources will also speed the identification of genes conferring useful traits that can be incorporated into breeding programs.



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 *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 *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 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.



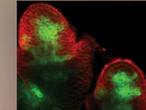
UniformMu: An inbred transposon population is used for functional genomics (Image: A. Mark Settles with Donald R. McCarty, Karen E. Koch, L. Curtis Hannah, University of Florida).



mtmDB: Mutations, such as in *branched silks (bdt)* 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 database, 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).

Maize