

# Putting the Function in Maize Genomics

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## Abstract

The 51st Maize Genetics Conference was held March 12–15, 2009 at Pheasant Run Resort in St. Charles, Illinois. Nearly 500 attendees participated in a scientific program (available at [http://www.maizegdb.org/maize\\_meeting/2009/](http://www.maizegdb.org/maize_meeting/2009/)) covering a wide range of topics which integrate the rich biology of maize with recent discoveries in our understanding of the highly dynamic maize genome. Among the many research themes highlighted at the conference, the historical emphasis on studying the tremendous phenotypic diversity of maize now serves as the foundation for maize as a leading experimental system to characterize the mechanisms that generate variation in complex plant genomes and associate evolutionary change with phenotypes of interest.

**C**HARLES DARWIN (1868) noted that “Maize has varied in an extraordinary and conspicuous manner.” The study of phenotypic diversity and its causal basis has long been a primary focus of maize geneticists. The scientific advances reported at the 51st annual Maize Genetics Conference held near Chicago in March, 2009, reflect efforts to understand how maize diversity is generated and contributes to phenotypes of importance to plant biology and crop improvement.

## Maize Genome Structure, Annotation, and Dynamics

A primary topic of interest was the status of maize genome sequencing projects. Doreen Ware (Cold Spring Harbor Laboratory) provided an update on the draft genome of the B73 inbred line, where nearly 17,000 assembled BAC sequences anchored to the maize physical map are available through the ever-improving genome browsers at [www.maizesequence.org](http://www.maizesequence.org) and MaizeGDB (<http://www.maizegdb.org/gbrowse>). Comparative analyses reveal a dramatic increase in retrotransposon density near breaks in synteny with genomes of related grasses, suggesting a role for these repeated sequences in mediating chromosomal rearrangements. Recognizing the expected structural diversity of the maize genome and the power of new short-read sequencing technologies, Dan Rokhsar

Published in *The Plant Genome* 2:103–106. Published 10 July 2009.  
doi: 10.3835/plantgenome2009.06.0004ed  
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677 S. Segoe Rd., Madison, WI 53711 USA  
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**Abbreviations:** NAM, nested association mapping.

(Department of Energy Joint Genome Institute) reported the sequence of the Mo17 inbred line that represents a different major heterotic group historically used with B73 to produce commercial maize hybrids. Using a whole-genome shotgun approach and 454 pyrosequencing, more than 25 Gbp of sequence and an estimated 11X coverage of the Mo17 genome has been produced that reveals excellent alignment with the B73 draft sequence, yet ample numbers of single-nucleotide polymorphisms were identified, as well as reads that appear unique to Mo17. The Mo17 sequence is available through the genomics portal at [www.phytozome.org](http://www.phytozome.org) (verified 8 June 2009). A third research group represented by Octavio Martinez (National Laboratory of Genomics for Biodiversity, Mexico) described analysis of sequences generated from Palomero Toluqueno, a popcorn landrace chosen for its smaller genome size. An assembly of the gene space produced nearly 400,000 unique sequences representing 325 Mb, and confirmed a lower repeat content for Palomero Toluqueno relative to B73. Michael Gore and Robert Elshire of Ed Buckler's group (USDA-ARS and Cornell University) presented initial results from resequencing the 27 inbred founders of the Nested Association Mapping panel using restriction-enzyme reduced representation libraries and next-generation deep sequencing technologies. In addition to providing large numbers of candidate polymorphic markers for genetic mapping, insights are gained regarding the evolution of major repeat elements, the distribution of recombination, and patterns of genetic diversity in maize at a genomic scale.

Just as important to most meeting attendees were the presentations about tools and resources for functional annotation of maize sequences. Yujun Han (University of Georgia) presented the TARGeT web-base pipeline for using a query sequence to retrieve related family members within the maize genome and rapidly build phylogenetic trees. Updates were provided on information and resources for maize genomics research housed at the National Center for Biotechnology Information (NCBI), Gramene ([www.gramene.org](http://www.gramene.org); verified 8 June 2009), MaizeSequence.org, MaizeGDB, PlantGDB, the Plant Expression Database (PLEXdb) and POPCorn, the Project Portal for Corn. A panel discussion and open forum was also held to discuss approaches and best practices for community-driven annotation of the maize genome that facilitates turning sequence information into knowledge.

The dynamic nature of the maize genome was highlighted in numerous presentations. Not surprisingly, transposon activities appear to play a major role in restructuring chromosomes, centromere function and evolution, and patterns of gene expression. However, Ashley Lough (University of Missouri) documented differences in the transfer of mitochondrial DNA to the maize nuclear genome that can serve as another source

of genetic diversity. Like transposons, epigenetic phenomena were initially characterized in maize and also contribute to phenotypic variation. Specific examples include the specification of centromere activity (Fangpu Han, University of Missouri), allele-specific imprinting in maize embryos (Stefan Scholten, University of Hamburg), and changes in the expression of thousands of genes in the maize *mediator of paramutation* (*mop1*) mutant that is defective in a putative RNA-dependent RNA polymerase functioning in RNA silencing (Yi Jia, Iowa State University).

### Functional Variation in Maize Genes

Functional genomics approaches are being increasingly applied to investigate many aspects of maize biology. A plenary talk by Joe Ecker (Salk Institute) illustrated how short-read deep sequencing technologies are revolutionizing the analysis of variation in nucleic acid samples associated with a wide range of cellular processes in *Arabidopsis*, extending beyond the genome and transcriptome to include epigenetic modifications (e.g. the “fifth base” methyl cytosine), protein-DNA interactions, and even protein-protein interactions. Sequence-based indices of transposon insertion collections were described for *Ds* (Erik Vollbrecht, Iowa State University) and *Mutator* (Susan Latshaw, University of Florida and Alice Barkan, University of Oregon). “Digital” gene expression profiling by deep-sequencing technologies was presented for maize leaf development (Tom Brutnell, Cornell University), root hairs (Charles Hunter, University of Florida), unfertilized ovaries (Bryan Penning, Purdue University), comparisons of the *ramosa3* mutant with wild-type inflorescences (Andrea Eveland, Cold Spring Harbor Laboratory), genes expressed in shoot apical meristems of maize and teosinte (Li Li, Iowa State University), and small RNAs in a maize hybrid and its inbred parents (Wes Barber, University of Illinois).

Maize research continues to identify genes that function in metabolic, developmental, and cellular pathways. Curt Hannah (University of Florida) opened the meeting with a review of ADP-glucose pyrophosphorylase and its key role in starch biosynthesis, and a variety of informed strategies to improve the properties of the enzyme and enhance maize grain yield. The final plenary talk by Marja Timmermans (Cold Spring Harbor Laboratory) detailed a series of experiments showing that adaxial-abaxial leaf polarity in maize is established through the action of opposing small regulatory RNAs and their target transcription factors. Inna Golubovskaya (University of California-Berkeley) described a collection of mutations in at least 35 genes affecting meiosis. The Maize Genetics Conference often features the molecular cloning of one or more genes associated with classic mutant phenotypes. For 2009, the *Grassy tillers1* locus, originally described in 1967

(Shaver, 1967), was determined to encode a homeodomain protein controlling tiller number and branch length (David Jackson, Cold Spring Harbor Laboratory). In addition, the *ragged seedling2* leaf patterning mutant results from a mutation in an ARGONAUTE7-like protein predicted to function in the production of trans-acting small interfering RNAs (Ryan Douglas, Cornell University). The molecular basis for four other recently described mutant phenotypes was also reported: *barren stalk fastigate1* encodes an AT-hook DNA-binding protein required for ear formation (Andrea Gallavotti, University of California-San Diego), the *vanishing tassel2* gene functions in auxin biosynthesis (Kimberly Phillips, Pennsylvania State University), altered activity of an ADP-ribosylation factor GTPase activating protein conditions the *Discolored1* kernel mutant phenotype (Elizabeth Takacs, Cornell University), and the *camouflage* mutation (Mingshu Huang, Pennsylvania State University) results from the first characterized genetic defect in plants for porphobilinogen deaminase of the heme biosynthetic pathway.

The mapping and analysis of quantitative trait loci formed the largest category of presentations, which emphasized not only the application of maize genetics research to crop improvement but also the increased interest in QTL mapping as an approach to gene discovery. A growing number of QTL studies are being conducted with community mapping resources such as the intermated B73 × Mo17 recombinant inbred lines and the nested association mapping (NAM) population, each of which offer the potential to resolve QTL to individual genes when integrated with increasing numbers of SNP markers. QTL were identified that contribute to measured variation for agronomic traits such as flowering time, shoot morphology, drought tolerance, nitrogen utilization, and reduced stalk or root lodging. QTL controlling resistance to insect pests (e.g. Western corn rootworm beetle, *Diabrotica virgifera*) and most of the major fungal diseases of maize were also reported. Other studies investigated QTL affecting grain composition and perhaps the most complex of all quantitative traits, heterosis. In addition, QTL mapping approaches are being applied to molecular phenotypes such as carbon/nitrogen metabolites (Nengyi Zhang, Cornell University) and RNA expression (Ruth Swanson-Wagner, Iowa State University and Yuhe Liu, University of Illinois) that lie closer to relevant gene action than morphological or visual traits.

### Beyond Maize Genetics

Although much of the science presented at the Maize Genetics Conference indeed focused on maize, research was also presented on relevant topics being studied in *Arabidopsis* and other grasses such as rice, sorghum and switchgrass. In addition to the “Arabidomics” perspective

offered by Joe Ecker, Luca Comai (University of California-Davis) gave a plenary talk on the consequences of polyploidy for dosage-sensitive regulatory networks, in particular chromatin modifications and non-additive regulation associated with hybridization and heterosis.

Maize is a crop of global economic and cultural importance and due to its diversity of visually striking phenotypes, also serves as an excellent vehicle to communicate the benefits of plant science and agricultural research. This message continues to be conveyed by advo-

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cates such as the National Corn Grower’s Association, which spearheaded the formation of the National Plant Genome Initiative in the late 1990s and was instrumental in support of the maize genome sequencing effort. For the first time, posters were invited from each of the attending agricultural biotechnology companies to describe career opportunities in their organizations. A number of posters also highlighted educational and public outreach efforts with a maize focus. Allison Phillips (Stanford University) described a program that prepares undergraduate students as mentors and teachers of plant biology to high school students. Anne Sylvester (University of Wyoming) uses maize as a culturally-relevant example for teaching genetics principles to students at Tribal Colleges. Michelle Denton (Cornell University) provided an overview of past and present “maize map gardens” that illustrate the maize genetic map by planting mutants in field plots in the order of their chromosomal positions, first established at Cornell University in the 1930s and continuing today at Florida A&M University.

The Maize Genetics Conference has a long history of encouraging attendance and participation of early-career scientists, which has contributed to the growth of the maize genetics and plant science research communities and helped develop the current generation of scientific leadership in the agricultural biotechnology industry. Among the 480 attendees of the 2009 Conference were 127 graduate students and 18 undergraduate students, each of whom were first authors of either short-talks (8) or poster presentations. Exposing these students to the broad scope of biology being

investigated with maize as an experimental system, the opportunities for discussion and networking among the community of maize scientists, and the connection to crop improvement efforts suggests that the future remains bright for new discoveries from continued study of the dynamic maize genome. We encourage all scientists interested in maize biology and crop improvement to consider attending the first Maize Genetics Conference held in Europe, at the relaxing venue of Riva del Garda in northern Italy, March 18–21, 2010. Conference details can be found at [www.maizegdb.org](http://www.maizegdb.org).

### Acknowledgments

Funding support for student attendance at the Maize Genetics Conference was provided by the National Science Foundation (award MCB 0925240), Monsanto Company, Pioneer Hi-Bred International, Inc., Syngenta, Dow AgroSciences, BASF Plant Sciences, and the National Corn Growers Association. The authors also acknowledge the efforts of the entire Maize Genetics Steering Committee in organizing an informative and enjoyable conference

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