MEETING REPORT

Maize Genetics 2003

Maize has importance both as a crop species and as a model system for research into grass genetics and plant development. This year, ~500 academic and industry researchers and students gathered from March 13 to 16 at the Grand Geneva Resort in Lake Geneva, Wisconsin, for the 45th annual Maize Genetics Conference. In this brief report, I present just a few highlights from the many excellent presentations given by ~35 speakers and in >200 posters. A complete set of abstracts can be accessed at http://www.agron.missouri.edu/.

SPIKELET DEVELOPMENT

Grass inflorescences are characterized by the development of a compact floral branch called a spikelet. In recent years, a number of genes that control spikelet development and morphology have been identified (Figure 1). George Chuck (Plant Gene Expression Center, Albany, CA) spoke about the control of spikelet meristem development by the branched silkless1 (bd1) gene. Mutations in bd1 alter spikelet meristem identity and cause the formation of indeterminate branches (Figure 1). The bd1 gene encodes an ERF transcription factor that is expressed in a distinct domain of the spikelet meristem. Putative orthologs of bd1 were cloned from 16 different grass species that exhibit highly divergent spikelet structures (such as rice and sorghum) and yet show an expression pattern similar to that of maize, suggesting that bd1 function is highly conserved among the grasses and is critical for spikelet formation (Chuck et al., 2002).

Erik Vollbrecht (Cold Spring Harbor Laboratory, NY) discussed the function of ramosa (ra) genes in regulating branch length in maize and other cereals. Mutations in ra1 or ra2 genes transform second-order branches in the maize inflorescence from short to long. ra2 functions to regulate the accumulation of ra1 transcript, defining a single pathway that regulates branch determinacy. Within maize, patterns of nucleotide diversity at ra1 indicate that the gene experienced a selective sweep during domestication or recent evolution. More broadly, comparative sequence and expression analyses of putative ra1 orthologs in divergent grass species suggest a general role for the ra genes in regulating branch length and implicate modulation of the ra pathway in the evolution of grass inflorescence diversity.

Peter Bommert (University of Cologne, Germany) presented collaborative research between Wolfgang Werr’s and Sarah Hake’s groups showing that the thick tassel dwarf1 gene (td1) is a potential maize ortholog of the Arabidopsis CLAVATA1 (CLV1) gene, a Leu-rich repeat receptor kinase that functions in aboveground meristems to control stem cell number. Mutations in genes involved in the CLV signaling pathway lead to either enlargement or fasciation of shoot meristems, thus resembling td1 mutants of maize, which exhibit fasciation of male and female inflorescence meristems. This work supports the hypothesis that the CLV signaling pathway generally is conserved in angiosperms.

MAIZE ORIGIN REVISITED

The maize genome is thought to have a tetraploid origin arising from hybridization and genomic fusion of diploid parents, consistent with a haploid chromosome number of 10 as opposed to the more typical number of 5 for other members of the grass subfamily Andropogoneae and the presence of two unlinked copies of many genes. In their seminal work on the origin of the maize genome, Gaut and Doebley (1997) suggested a segmental allotetraploid mode of evolution, based on analysis of synonymous substitution distances (dS) of 14 duplicated maize loci that appeared to show a bimodal dS distribution. Segmental allotetraploidy arises from the hybridization of species whose genomes are partially distinct, in contrast to allotetraploidy involving the fusion of genomes of two distinct species and autotetraploidy involving a doubling of chromosome number within a species. Both genomic allotetraploidy and autotetraploidy are predicted to show unimodal dS distribution patterns around a mean that corresponds to the divergence time of the two distinct diploid ancestors (allotriploidy) or the time of the switch from tetrasomic to disomic inheritance (autotriploidy). Segmental allotetraploidy essentially represents a combination of allotetraploidy and autotetraploidy; thus, the dS distribution pattern is predicted to

Figure 1. Maize Spikelet Mutants.

At top left, an ear of the branched silkless1 (bd1) mutant (left) is silkless and many branched (a wild-type ear is shown at right). At top right, mutations in ramosa1 (ra1) transform short branches to long in the upper tassel (left; cf. the wild type at right) and in the ear. At bottom, the thick tasseled dwarf1 (td1) mutant is shown. (Photographs courtesy of George Chuck [bd1], Erik Vollbrecht [ra1], and Peter Bommert [td1].)
be bimodal, with one set of sequences grouped around a mean representing the time of divergence of the diploid ancestors and the other representing the time of the switch from tetrasomic to disomic inheritance.

The model of Gaut and Doebley (1997) also suggested that one of the two ancestral diploids was related more closely to modern sorghum than it was to the other ancestral diploid and postulated three distinct divergence/duplication times: 20.5 million years ago, corresponding to the divergence of the maize and sorghum ancestral species; 16.5 million years ago, corresponding to the divergence of modern sorghum and the sorghum-like maize subgenome; and 11.4 million years ago, corresponding to the switch from tetrasomic to disomic inheritance after genomic hybridization within the maize genome.

Volker Brendel (Iowa State University, Ames) described a recent study that made use of improved distance estimation methods to reexamine the same data set analyzed by Gaut and Doebley (1997) and to further analyze an enlarged set of putative duplicated maize gene pairs. This study found dS to be distributed normally around a single mean, interpretable as a single duplication event that occurred ~16 million years ago, which is close to the time of speciation between maize and sorghum.

**RECOMBINATION: MEET ME AT THE bronze LOCUS**

The maize genome consists of small islands of gene-coding regions in a vast sea of highly repeated sequences. These repeat sequences are largely made up of retrotransposon clusters that typically display a nested organizational structure. Hugo Dooner (Rutgers University, Piscataway, NJ) described work that characterized recombination in and around the bronze (bz) locus, which is part of a gene-rich island and a recombination hot spot in the maize genome. The bz gene island was found to have a particularly high gene density (higher than the average for the Arabidopsis genome), which may help explain the high recombination rate observed within this region. In contrast to the gene island, the retrotransposon clusters immediately flanking the bz region were found to be recombinationally inert. Analysis of this region in different inbred lines revealed two rather surprising findings. First, the bz region exhibited considerable variability in gene content between lines, and some genes were completely absent from certain lines. This degree of variability has intriguing theoretical and practical implications, such as providing an explanation for observations of heterosis in hybrid vigor across multiple inbred lines. If genes within the bz region (or other similar gene-rich islands) contribute to hybrid vigor and there is variability in gene content between different lines, then heterosis of hybrid vigor would be expected. Second, the makeup of retrotransposon clusters showed a high degree of variability between different lines, such that the makeup of nested clusters (e.g., specific classes of retrotransposons) immediately adjacent to the bz gene island were completely different in several different inbred lines. These observations are indicative of a high degree of plasticity in the organization of the maize genome (Fu and Dooner, 2002).

**LESSONS FROM RICE**

Susan McCouch (Cornell University, Ithaca, NY) spoke about the use of recombination as a powerful approach for identifying and cloning genes underlying quantitative trait loci (QTLs) in rice. McCouch and colleagues have constructed high-density molecular maps in rice based on microsatellite markers, which have allowed the rapid identification of numerous genes underlying QTLs. Much of McCouch’s talk focused on understanding QTLs that have a transgressive effect, meaning that they produce a phenotype in the progeny of a cross that goes beyond the limits observed in the parental lines. For example, *Oryza rufipogon*, a wild relative of domestic rice (*O. sativa*), has a mean heading date that is later than that of most elite inbred varieties of *O. sativa*. Nonetheless, introgression of a QTL for heading date from *O. rufipogon* into an elite inbred background resulted in a mean heading date that was significantly earlier than that of either parent. This phenomenon is not understood entirely, but it is believed to arise because multiple factors interact to produce a particular phenotype. Thus, certain elite inbred lines of domestic rice have other factors that affect heading date that are not shared by *O. rufipogon* but that can be combined with an allele from the wild relative to affect heading date in a manner not observed in either of the parental lines. There are numerous other examples of QTLs from wild relatives that show transgressive effects when introgressed into elite domestic varieties, highlighting the possibility of recovering agronomically useful alleles from wild relatives of crop species.

**GENOMICS RESOURCES**

**Consortium for Maize Genomics**

Catherine Whitelaw (The Institute for Genomic Research [TIGR], Rockville, MD) and Brad Barbazuk (The Donald Danforth Plant Science Center, St. Louis, MO) presented an overview of the Consortium for Maize Genomics, a National Science Foundation–funded collaboration between TIGR, the Danforth Plant Science Center, Purdue University, and Orion Genomics that is designed to develop high-throughput strategies to isolate and sequence maize genes. The group is evaluating the maize “gene space” by analyzing sequence obtained from methylation-filtered libraries produced by Orion Genomics and high-Cot libraries produced by Jeff Bennetzen and colleagues at Purdue University. These strategies are being used to screen out the bulk of highly repetitive (non-gene-coding) sequence, which may constitute up to 85% of the maize genome, to facilitate the sequencing of gene-rich regions and thus provide the most rapid and cost-effective alternative to whole-genome sequencing. Methylation filtration is used to create libraries of in-
serts composed of nonmethylated maize genomic DNA. It has been shown that maize gene-rich islands are largely unmethylated, in contrast to highly repetitive regions, which exhibit a high degree of methylation. High-Cot selection creates libraries of low-abundance sequences in the genome, exploiting the relatively low abundance of gene sequences compared with highly repetitive retrotransposon sequences. Researchers at TIGR are conducting sequencing, assembly, and annotation of up to 500,000 clones each from the methylation-filtered and high-Cot libraries. The staff at the Danforth Center will provide additional annotations and an overall analysis of gene hit rate and gene coverage, participate in identifying method biases, and anchor the assemblies to the physical map. Sequencing has been completed on ~150,000 clones to date, and the goal is to generate a draft sequence of the maize gene space within 2 years. More information can be found at http://maize.danforthcenter.org/ and at http://www.tigr.org/tdb/tgi/maize.

MaizeGDB
Trent Seigfried (Iowa State University, Ames) introduced the Maize Genetics/Genomics Database (MaizeGDB), a U.S. Department of Agriculture/Agricultural Research Service–funded project slated to provide a comprehensive online workbench for maize researchers that will integrate the data contained in the two existing major maize databases, MaizeDB and ZmDB. MaizeGDB curators will work closely with the maize research community and a nationwide MaizeGDB Steering Committee to develop a user-friendly interface to provide easy access to maize genetics and genomics data and to facilitate data analysis. The MaizeGDB World Wide Web site at http://www.maizegdb.org/ contains an online tutorial and a user survey in addition to numerous links to maize data centers and information. The curators are seeking as much feedback as possible from all users. Check it out today!

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REFERENCES