

an undefined but important role in the ABA-guard cell ion channel signalling pathway.

Vesicle fusion or ion channel regulation?

There is clearly some accomplished science responsible for delineating this pathway, but what does it all mean? One relevant observation is that syntaxins (or at least some of them) might not directly regulate vesicle fusion but instead regulate channel activity. Almost coincident with the appearance of the article by Blatt's group was a report that in yeast, SNARE complex formation, which occurs during vesicle docking, results in the opening of a Ca²⁺ channel⁶. This in turn promotes the vesicle fusion step⁷. Another syntaxin has been shown to regulate the cyclic AMP-gated chloride channel encoded by the cystic fibrosis gene⁸. An unusual feature of Nt-Syr1 is that it has a putative Ca²⁺-binding domain². This is interesting when you remember that ABA signals guard cell opening via changes in intracellular Ca²⁺ (Ref. 9). Furthermore, the massive change in plasma membrane surface area during guard cell opening and closure presumably involves large scale vesicle trafficking^{10,11}.

Why ABA might regulate guard cell channels through a vesicle docking protein is, therefore, still mysterious, but this effect of a SNARE is not entirely without precedent. Thus, there appears to be much to keep the plant cell biology community busy, and perhaps now, at last, guard cell physiologists and 'vesicle trafficking people' will share a common goal.

Acknowledgements

My thanks to Nikki James for her useful comments.

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Jumping genes and maize genomics

One of the most exciting aspects of the recent Maize Genetics conference* was a growing appreciation of the impact that the National Science Foundation's Plant Genome Initiative will have on advancing maize as a model system. Given the current projections, maize will become the largest crop worldwide within a few years. It is vital that such a major crop – and model genetic organism – should have a well-defined genome. An evening workshop described the projects currently funded by the Plant Genome Initiative (for more information see <http://www.nsf.gov/bio/pubs/awards/genome98.htm>). One project headed by Ed Coe, Jr (University of Missouri, Columbia, MO, USA) will be to develop a coordinated genetic and molecular map to which a BAC library can be anchored. Several thousand new simple sequence repeat (SSR) markers will be developed and used to locate 3400 phenotypically recognized mutations on the map. This resource will set the stage for the genetic ordering of a collection of ESTs, which are being sequenced in a project headed by

Virginia Walbot (Stanford University, CA, USA). A complementary study directed by Zac Cande (University of California, Berkeley, CA, USA) will integrate the physical features of the chromosomes with the genetic information. This project will help to elucidate the global position of genes and repetitive elements that could shed light on the

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mechanism of recombination and provide the tools to study the action of chromosomes in interphase, mitosis and meiosis.

The sequence data, together with an insertion collection produced by a modified *Mutator* transposable element, will be used to identify all the genes in maize. This element has been modified to carry a bacterial origin of replication and a selectable marker. Its transposition is revealed by its excision from a

maize visible marker. It has been transformed into maize and used to recover numerous sequences following somatic transpositions. A further goal of this project is to identify ~150 000 germinal insertions and sequence the adjacent DNA to generate a virtual 'knock-out' center in which one can screen the database with a sequence of interest and identify insertion events. A complementary approach, headed by Robert Martienssen (Cold Spring Harbor Laboratory, Cold Spring Harbor, NY, USA), is to generate a population that carries a *Mu* insertion into every maize gene. Once the collection of genes is known, the task of ordering them on the chromosomes will be aided by a method being developed by Howard Rines and Ronald Phillips (University of Minnesota, St Paul, MN, USA). They have produced a collection of oat stocks that carry a single maize chromosome in addition to the oat genome. The individual addition lines were irradiated to generate a collection of small fragments interspersed within the oat chromosomes. By probing a panel of these DNAs, individual ESTs can be mapped with great precision. These tools and others will set the stage for a myriad of functional genomic endeavors.

The use of another class of transposons, miniature inverted repeat transposable elements

*41st Maize Genetics Conference, Lake Geneva, Wisconsin, USA, 11–14 March 1999 (see http://www.agron.missouri.edu/maize_cooperators.html for abstracts).

(MITEs), for gene identification and molecular mapping markers was discussed by Sue Wessler (University of Georgia, Athens, GA, USA). Features of MITEs in maize (~5000–15 000 per haploid genome, sequence similarity, preference for insertion in genic regions and the high degree of polymorphism among maize inbred lines) have been combined with a modified AFLP procedure (called transposon display) to provide markers anchored preferentially in genic regions. The isolation of MITEs from other plant genomes will extend this tool to other species.

Gene silencing

Many natural cases of gene silencing were first described from studies based on the behavior of maize transposable elements and the phenomenon of paramutation – the heritable silencing that follows the association of a silencing allele and a sensitive allele in a heterozygote. A synthesis of several reports at the meeting indicates that some forms of transgene silencing and the various cases of paramutation are mechanistically related. Paramutation has been described at the *r*, *b* and *pl* loci. A new case was described for the *p* locus by Wolfgang Goettel and colleagues (Rutgers, The State University of New Jersey, Piscataway, NJ, USA). Interestingly, all four loci are transcriptional regulators of the anthocyanin or phlobaphene pigment pathways, which are expressed in various tissues of maize. For studies of the regulation of the *p* gene, Lyudmila Sidorenko and colleagues (Iowa State University, Ames, IA, USA) produced transgenes with promoter fragments of the *p* locus driving the expression of GUS. This transgene silenced a functional copy of the *p* gene, *P-rr*. When this silenced endogenous gene was crossed to *P-rr* again, the silencing was transferred to the homologous allele, which is consistent with paramutation, even though the transgene had segregated away in meiosis. These observations establish a direct link between homology-dependent gene silencing and paramutation. The reports of Jane Dorweiler and colleagues (University of Arizona, Tucson, AZ, USA) described mutations that affect the action of paramutation, with a dominant and a recessive mutation that each block paramutation. Although paramutation at the *r*, *b* and *pl* loci have distinctive features that have led some investigators to wonder whether they represent independent mechanisms, the recessive mutation blocks paramutation at all three loci. Together, these studies not only indicate a connection between some forms of transgene silencing and paramutation, but also among paramutation cases as a whole.

Developmental programs

Although a significant part of the meeting was

focused on the potential of coordinated functional genomics programs to change the way in which we identify genes and correlate mutant phenotypes with gene function – traditional transposon tagging and homology-based cloning procedures continue to uncover interesting aspects of maize developmental biology. Phil Benfey (New York University, USA) discussed the role of genes that regulate radial patterning in both maize and *Arabidopsis*. In the *SCARECROW* (*SCR*) mutant of *Arabidopsis*, the root contains a layer of cells that has attributes of both cortex and endodermis. Thus, it has been proposed that *SCR* regulates radial patterning in the root by controlling the asymmetric division that contributes to the formation of distinct endodermal and cortical cell layers. Recent work indicates that it might also regulate the formation of bundle sheath cells in the *Arabidopsis* shoot. The *Arabidopsis* gene, which encodes a putative transcription factor, has been used to isolate the *SCR* ortholog (*ZmSCR*) from maize, which might also affect radial patterning. Viewed in longitudinal sections, *ZmSCR* expression is seen throughout the root endodermal layer, even as it traverses the quiescent center (QC). This expression pattern allowed an analysis of cell layer organization during QC regeneration. When the QC was removed, the new line of *ZmSCR* expression paralleled the shape of the root edge but moved inward relative to the line of expression seen before disruption. These results are consistent with cell-to-cell signaling playing a central role in the regeneration process.

In addition to gaining an understanding of cellular differentiation processes, considerable effort continues to be invested in trying to understand how the switch occurs from indeterminate shoot growth to determinate lateral organ growth. It has been known for some time that the acquisition of lateral organ identity is correlated with the disappearance of *knotted1*-like homeobox (*knox*) gene products in founder cells of the meristem. Data presented by Mike Freeling (University of California, Berkeley, CA, USA) and Mike Scanlon (University of Georgia, Athens, GA, USA) demonstrated that at least two genes, *rough sheath2* (*rs2*) and *semaphore1* (*sem1*) act to repress *knox* gene expression in lateral organs. Mike Freeling described how *rs2*, which encodes a *myb*-like transcription factor, has been shown to maintain the repression of *knox* genes in leaf primordia but that it is not involved in the initial down-regulation of *knox* genes in founder cells. Thus, a second mechanism acts to suppress *knox* gene expression during leaf initiation. The *sem1* gene was recently cloned by Mike Scanlon by transposon tagging. It will be interesting to determine whether *sem1* encodes a transcrip-

tion factor with sequence similarity to *rs2* and, more importantly, whether it complements *rs2* gene action by acting during leaf initiation.

Maize mitochondria

In addition to the nuclear genome, maize is particularly suited for the study of mitochondrial and plastid genomes. Patrick Schnable (Iowa State University, Ames, IA, USA) described the transposon tagging, cloning and biochemical analysis of *rf2*, a restorer of a mitochondrial lesion, cytoplasmic male sterility, type T. The *cmsT* phenotype is caused by a chimeric gene in the mitochondria when two nuclear genes, *rf1* and *rf2* are recessive. The *rf2* gene encodes a mitochondrial aldehyde dehydrogenase, whose expression is consistent with a role in restoring fertility. Determination of the relationship to the mitochondrial lesion represents an interesting area for future investigation. Using another type of male sterility, *cmsS*, Christine Chase (University of Florida, Gainesville, FL, USA) described a system to identify and study numerous nuclear restorers that will identify nuclear genes that affect mitochondrial functions. J. Clinton Bailey and colleagues (University of Missouri, Columbia, MO, USA) reported that novel small mitochondrial subgenomes occur in a nuclear background that promotes a variety of new mitochondrial mutations. These approaches should identify many of the nuclear genes with functions that affect the mitochondrial genome.

Acknowledgements

Our thanks to Julie Vogel (Dupont Agricultural Biotechnology, Newark, DE, USA) and Cliff Weil (University of Idaho, Moscow, ID, USA) for organizing a terrific meeting.

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