Meeting report

Model legumes in the limelight

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A report of the Molecular Genetics of Model Legumes meeting, John Innes Centre, Norwich, 24-28 June, 2000.

Leguminous plants provide protein and oil to humans and animals and fix atmospheric nitrogen, and are thus of considerable economic, ecological and biological interest. Most crop legumes are polyploid, and are not amenable to molecular genetic studies. Two legume species, however - the fodder crop *Medicago truncatula* (barrel medic) and the wild species *Lotus japonicus* (trefoil) - have recently emerged as model legumes because of their short generation times, diploidy and small genomes. The availability of these legumes enable investigation into aspects of plant biology that *Arabidopsis* lacks, such as symbiosis between plants and microbes. Recent research on these model systems was reported at the meeting.

Symbiosis and disease resistance

Because of their association with nitrogen-fixing bacteria, legumes are crucial in understanding the interplay between symbiont and host plant in the establishment of symbiosis. Using arbuscular mycorrhizal (AM) fungi as the symbiont, Maria Harrison (Samuel Roberts Noble Foundation, Oklahoma, USA) has identified *M. truncatula* mutants that fail to support the formation of fungal hyphal ingrowths (arbuscules) in the plant's cells (Figure 1). She also found that some of these mutants fail to form a symbiotic relationship with the nitrogen-fixing bacterium *Sinorhizobium meliloti*, indicating an overlap between the two symbiosis pathways. Similarly, Martin Parniske (John Innes Centre, UK) reported the identification of sixteen *L. japonicus* mutants, falling into six complementation groups, all of which fail to form symbiotic relationships with both rhizobia and AM fungi. Igor Tikhonovich (All-Russia Research Institute for Agricultural Microbiology, Russia) described various pea (*Pisum sativum*) mutants that cease nodule development at different stages. By exploiting the natural genetic variability in *M. truncatula*, Jean Denarie and Thierry Huguet (CNRS-INRA, Tolouse, France) have identified ecotypes that fail to recognize different rhizobial nod (nodu-

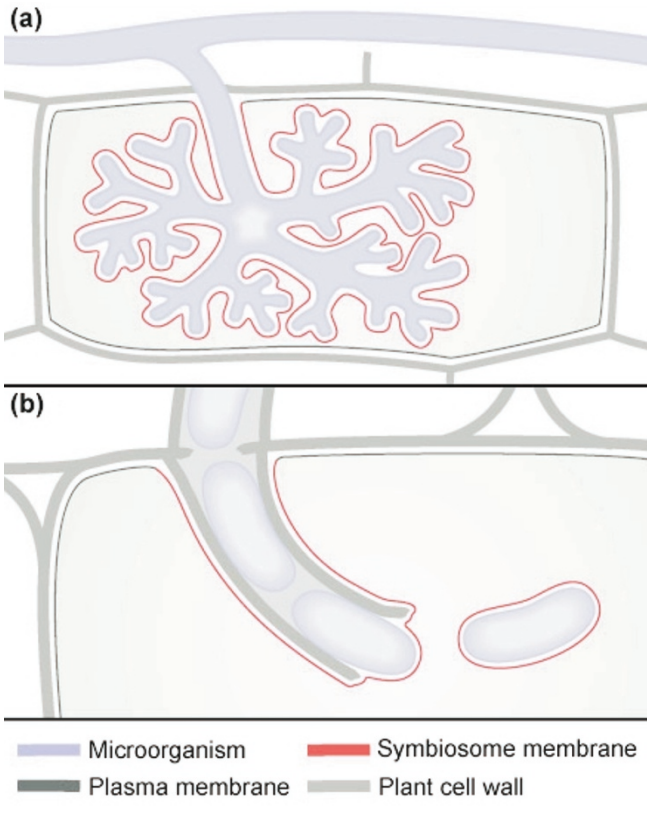

Figure 1
Examples of endosymbiotic interactions. (a) An arbuscule (fungal hyphal ingrowth) within a root cortical cell (in this case of *Glomus* sp.). (b) An infection thread and bacteroid within a root nodule cell. Note that the perimicrobial membrane (symbiosome membrane; red) is of plant origin. This figure was prepared by Eva Wegel (John Innes Institute, UK) and is reproduced with permission from *Curr Opin Plant Biol* 2000, **3:**320-328.

lation) factors, which are involved in the specific recognition of the host and symbiont. This will help the cloning of host genes involved in the specific recognition of the symbiont.

Like symbiosis, disease resistance is the result of an interaction between a host plant and a microorganism. In symbiosis, however, the plant tolerates the presence of a microorganism and accommodates it within its tissues, while in disease resistance it does not. In order to determine features common to these two interactions, Doug Cook (Texas A & M University, USA) has tested the *M. truncatula* early nodulation mutant, *dmi1-1,* and the hyper-nodulating, ethylene-insensitive mutant, *skl-1*, against the fungal pathogens *Rhizoctonia solani* and *Phytophthora medicaginis*. Whereas *dmi1-1* is not altered in its interaction with both *R. solani* and *P. medicaginis* compared with wild-type *M. truncatula*, *skl-1* is more susceptible to *P. medicaginis*. Analysis of the responses of other nodulation mutants to pathogens will help define the extent of overlap between symbiosis and disease resistance.

Legumes offer unique opportunities in the area of plant-pathogen interactions. Although *Arabidopsis* is susceptible to nematodes, an absence of functional polymorphisms for nematode infection prevents its use to study the genetics of plant-nematode interactions. Charlie Opperman (North Carolina State University, USA), Cook and I reported several *M. truncatula* ecotypes that are resistant or susceptible to root-knot nematode (*Meloidogyne* sp.), which paves the way towards studying plant-nematode interactions genetically. Matthias Hahn (Konstanz University, Germany) reported variation in *M. truncatula* susceptibility to rust *(Uromyces striatus*) infection.

Gene tagging

Genes that control essential plant processes cannot be identified by induced mutagenesis, as their complete knockout is lethal. Similarly, knocking out a gene that is redundant with others by induced mutagenesis will have little or no effect, making study of that gene difficult. This problem can be overcome by using enhancer traps or promoter traps that help to identify essential genes without knocking out their function. Judy Webb (University of Wales at Aberystwyth, UK) described one promoter-trapped *L. japonicus* plant, T-90, which expressed the reporter gene in root epidermis, root hairs and nodules in the presence of a symbiont but did not express it when a non-nodulating mutant symbiont was inoculated. The T-DNA insertion in T-90 is upstream of a gene encoding a calcium-binding protein, suggesting the involvement of this protein in symbiosis.

Genomics

As more people become interested in using model legumes in their research, it is imperative that all the genomic tools be in place for easy gene cloning. Niels Sandal (University of Aarhus, Denmark) and Shinji Kawasaki (National Institute of Agrobiological Resources, Tsukuba, Japan) independently reported the development of recombinant inbred lines from different *L. japonicus* ecotypes, construction of a linkage map with amplified fragment length polymorphism (AFLP) markers and construction of bacterial artificial chromosome (BAC) libraries. Huguet reported the development of recombinant inbred lines between four *M. truncatula* ecotypes and construction of a linkage map with AFLP and microsatellite markers for *M. truncatula*. Gyorgy Kiss (Biological Research Centre of the Hungarian Academy of Sciences, Hungary) described the development of a genetic map with restriction fragment length polymorphism (RFLP) and random amplified polymorphic DNA (RAPD) markers for diploid alfalfa *(Medicago sativa)*.

Functional genomics

Mutational analysis permits us to study only one gene at a time and does not provide information about all the genes that are expressed during a particular process. This information can be obtained by sequencing all the mRNAs that are expressed during the process. By sequencing expressed sequenced tags (ESTs) and expression profiling, Harrison has determined the changes in gene expression that occur during the *M. truncatula*-AM fungal symbiosis. Genes such as peroxidases and leucine-rich repeat receptor kinases are downregulated, whereas genes involved in cytokinin synthesis are upregulated. On the basis of EST sequencing and similarity searches, Satoshi Tabata (Kazusa DNA Research Institute, Japan) reported that around 36% of EST sequences obtained from a normalized *L. japonicus* cDNA library are novel and may be unique to legumes.

Proteomics

Another means of identifying all the genes involved in a plant process is to analyze the spectrum of proteins expressed in the cell using two-dimensional gels followed by mass spectrometry. Gerhard Saalbach (Riose National Laboratory, Denmark) has used this approach to identify the proteins present in the peribacteroid space and peribacteroid membrane of the rhizobial symbiosome, which is in intimate contact with the plant cell (see Figure 1). Thirteen different proteins of bacteroid origin, including malate dehydrogenase, three bacterial chaperonins and a bacterial homolog to plant disulfide isomerase, have been identified.

Exploitation of microsynteny

A knowledge of the synteny (that is, the existence of chromosomal regions containing the same genes in the same order) between model legumes and economically important legumes would help us to clone genes more easily from the latter, for which little genetic information is available. In addition, syntenic relationships will help us to understand

how crops evolved from the simpler model legumes. Nevin Young (University of Minnesota, St Paul, USA) has identified more than 50 contigs of around 150-200 kilobases in the soybean (*Glycine max*) genome that have synteny with *M. truncatula*. It is not yet known whether these syntenies are conserved in *L. japonicus*.

Clearly, studies of *M. truncatula* and *L. japonicus* are likely to prove invaluable both to understanding the basic biology of legumes and to improving leguminous crops.