

Meetings

Fungal biology: compiling genomes and exploiting them

12th European Conference on Fungal Genetics, Seville, Spain, March 2014

The 12th European Conference on Fungal Genetics (ECFG12) took place in March 2014. Every 2 years a European country welcomes this meeting, which is held in coordination with the Fungal Genetics Conferences that take place every 2 years in Asilomar (USA). This year over 700 participants from 40 countries gathered in Seville (Spain) to exchange ideas on the central theme of fungal genetics and general fungal biology including molecular and cell biology, genomics, evolution and biotechnology. The conference included plenary sessions in honor of three prominent fungal geneticists (Charles Yanofsky, John Clutterbuck and Claudio Scazzocchio), concurrent sessions such as the tremendous 'Fungal genomes: now what?', and six satellite meetings including the 4th Mycorrhizal Genomics Initiative Workshop (MGIW4). In the latter meeting, coordinated by Francis Martin (INRA, Nancy, France), approx. 30 junior and senior scientists discussed progress made on exploring the genome diversity of mycorrhizal fungi and debated future directions on how to use the current data sets to bridge mycorrhizal genomics, metagenomics and forest ecology. In this meeting report, we focus on the engaging discussions surrounding fungal genomes and their utilization.

'... the evolution of effectors is a key aspect to both speciation within symbiotic fungi as well as a determinant in host plant specificity.'

Fungal genomics moving forward

The last 10 years have seen the cost of sequencing complete genomes decrease at an incredible speed. This has led to an increase in the number of genomes sequenced in all the fungal tree of life as well as a wide variety of plant genomes. The increase in sequencing has permitted us to study the evolution of organisms on a genomic scale. A number of talks during the conference discussed the importance of transposable elements (TEs) that are present in almost all species of fungi. These TEs represent an especially large

percentage of genomic space in fungi that interact with plants. Thierry Rouxel (INRA, Nancy, France) showed the link between speciation in the *Leptosphaeria* complex and the expansion of TE families. For example in the *Leptosphaeria* complex, one species associated with oilseed rape has experienced a recent and massive burst of movement by a few TE families. The alterations caused by these TEs took place in discrete regions of the genome leading to shuffling of the genomic landscape and the appearance of genes specific to the species, such as effectors useful for the interactions with a particular plant (Rouxel *et al.*, 2011). Other presentations showed the importance of TEs in affecting genome organization. For example, in *Amanita* different species appear to have been invaded by different TE families (Veneault-Fourrey & Martin, 2011).

There were also many engaging oral presentations on the potential applications of the genomic data now available from multiple sources. These data enable inferences of how the genomic content and structure of fungi can impact interactions with, and response to, their hosts and environments. One particularly successful strategy has been using the newly available genes from phylogenomic studies to ask questions about how closely related fungal lineages developed different ecological strategies. Joey Spatafora (Oregon State University, Corvallis, OR, USA) discussed work on homologous nonribosomal peptide synthetase (NRPS) clusters in the Hypocreales. His team found that duplications, rearrangements, and fusions of conserved adenylation domains in derived members of close pathogenic relatives mirror host switches between plants, fungi, and insects. This work raises questions about the mechanisms involved in genome expansion, contraction, and rearrangement. It also raises the question concerning which of these processes most strongly influence shifts in host interactions and other changes in life strategies (Veneault-Fourrey & Martin, 2011). Francis Martin summarized analyses of several mycorrhizal fungal genomes from the Mycorrhizal Genomics Initiative (<http://mycor.nancy.inra.fr/IMGC/MycoGenomes/>), which is an ongoing multi-institution joint program with the JGI focused on sequencing mycorrhizal fungal species (Martin *et al.*, 2011). Large emerging patterns include losses in lignocellulolytic decomposition capabilities in several groups of ectomycorrhizal fungi compared to their saprotrophic ancestors. Interestingly, ericoid and orchid mycorrhiza retain the potential to decay most components of secondary plant cell walls. As more fungal genomes are sequenced through this, and other, initiatives it will be interesting to evaluate commonalities of genomic content and structure in addition to determining which aspects of fungal biology underwent convergent evolution in order to produce the mycorrhizal habit in phylogenetically distinct fungal lineages. Hanna Johannesson (Uppsala University, Sweden) and colleagues presented data comparing rates and locations of selection and recombination in nearly 100 *Neurospora tetrasperma* genomes. These data suggest population

level sweeps of entire mating-type chromosomes driven by introgression and ultimately fixations are detectable in some lineages (Nygren *et al.*, 2011). It has been demonstrated that variants in multi-allelic genes can selectively sweep through populations of many diverse organisms, and evidence for larger scale selective sweeps has recently emerged in several model organisms. The frequency of such sweeps and implications for the evolutionary trajectories of fungal groups with this capability are an exciting avenue for future research. Michael Brunner (Heidelberg Biochemistry Center, Germany) spoke about dynamics of light induced transcriptional re-profiling in *Neurospora*. He presented data suggesting that chromatin re-modification via interaction of GATA type transcription factor SUB1 with a putative acetyltransferase may facilitate access of the transcription factor White Collar Complex (WCC) to promoters of genes involved in the response. The epigenetic control of functional genes has been demonstrated in several other fungal groups, and in some instances appears to play an important role in symbiotic relationship establishment and maintenance (Soyer *et al.*, 2014). Future investigations into the extent of epigenetic control of fungal response to stimuli from the environment and other organisms will be informative into the question of how fungi regulate and strategically use their genomic contents. Jason Stajich (University of California, Riverside, CA, USA) discussed recent work on the evolution of multi-cellularity in fungi by comparing several genomes in lineages of Ascomycetes and Basidiomycetes that convergently gained multi-cellularity. Comparative analyses of genome content and organization revealed increases in copy number of signaling, perception, and cell wall gene families among others are likely involved in gain of multi-cellularity. The future sequencing of many genomes that falls along a spectrum of physical complexity will allow a more thorough analysis of the question, does complex trait gain most often result from genome content gain and loss, organization, or higher-level control or some combination of the three?

Deciphering the interactive toolbox one effector at a time

The conference was a stirring update on the progress in our understanding of effector biology in both pathogenic and mutualistic fungi. Effectors are small secreted fungal proteins that are used during the symbiotic interaction with plants to alter the physical or chemical environment of plant tissues to favor colonization. Sophien Kamoun (The Sainsbury Laboratory, Norwich, UK) took us back into the evolutionary past of the *Phytophthora* genus with his group's recent work with the EpiC1 effector (Dong *et al.*, 2014). They have shown that this effector evolved specific activities after a host jump and, through phylogenetic analysis, were able to predict the ancestral version of this effector and demonstrate how its activity had changed. This work has demonstrated that the evolution of effectors is a key aspect to both speciation within symbiotic fungi as well as a determinant in host plant specificity. This work, leaves the intriguing question: how many effectors are required before a fungus can colonize a new host?

Within the effector community one aspect of their biology has hampered the *in silico* annotation of their functions: very rarely do effectors encode conserved domains nor do they exhibit close homology with other proteins at the nucleotide level. Despite these differences, as more effectors are characterized, the more we find that they have similar biological activities or consequences. Alga Zuccaro's group (Max Planck Institute, Marburg, Germany) working with the effectors of *Piriformospora indica* is tackling just this problem. By taking effectors with no known homologues and by doing the tricky work of crystallization, her group is determining the three-dimensional (3D) structure of these effectors. And the results have been worth the effort. New data coming from Alga's group is now showing that there are conserved motifs between fungal effectors and other known proteins – even proteins from bacteria! These results would indicate that the next challenge of this field is to look to the arduous task of understanding the biology of our favorite effectors in 3D.

Back in the pathogenic camp, Shigeyuki Tanaka (Max Planck Institute, Marburg, Germany) gave a great talk concerning Tin2, one of the virulence promoting effectors of *Ustilago* (Tanaka *et al.*, 2014). In an interesting twist, this effector targets, and promotes, the production of anthocyanins in the host plant. While, at first, this seems like a rather wandering path toward assuring virulence, the metabolic reasoning behind this effect is brilliant. In promoting anthocyanin synthesis in infected leaves, the fungus is forcing the host plant to divert maximal levels of the precursor p-Coumaric acid toward a benign end-point and away from the lignin pathway. In depleting the host of lignin, *Ustilago* is able to form infection structures and hijack plant cellular functioning, a circumstance that would not happen if the host were able to lignify the infected tissues. This case study is very pertinent in highlighting the fact that effectors may not directly target problematic host pathways that would hurt their chances of colonization. Rather they may act upon a parallel pathway to indirectly aid the take-over of plant functioning. Thus, the only way to fully understand these complex problems is to have an intimate knowledge of the host biology as well as the fungal symbiont.

Typically in our areas of specialization, we choose to focus on the effectors of either pathogenic fungi or mutualistic fungi with very little crossover. With so many effectors to characterize this is a rational approach. If, however, we are to understand the full biological relevance of these intriguing proteins we must begin to cross disciplines and begin to work on a more unified vision of effector biology. Natalia Requena's presentation addressed just this point. In her group (Karlsruhe Institute of Technology, Karlsruhe, Germany) they are beginning to work on both pathogens and mutualists to begin the process of identifying common host proteins targeted by effectors from both lifestyles. While this work is still in its infancy, we await with great anticipation this next step in the study of these proteins. Will effectors from both lifestyles affect the same host proteins? If such host 'hub' proteins exist, will mutualistic and pathogenic effectors control their target in the same way or in opposing fashions? We anticipate the answer to these questions and so many more in 2 years in Paris at the 13th ECFG.

Acknowledgements

Many thanks to Krista Plett and Francis Martin for helpful comments on the manuscript. Thanks also to all who attended and gave freely of their data, thoughts and opinions. The authors acknowledge the Genomic Science Program (project 'Plant-Microbe Interactions'), US Department of Energy, Office of Science, Biological and Environmental Research, for supporting the authors' participation to this meeting, under the contract DE-AC05-00OR22725.

Jessy Labbé^{1*}, Jessie Uehling², Thibaut Payen³ and Jonathan Plett⁴

¹Biosciences Division, Oak Ridge National Laboratory, PO Box 2008, Oak Ridge, TN 37831-6422, USA;

²Biology Department, Duke University, Durham, NC 27708, USA;

³UMR 1136, INRA/Lorraine University, 'Tree-Microbe Interactions', Lab of Excellence ARBRE, INRA, Nancy 54280, Champenoux, France;

⁴Hawkesbury Institute for the Environment, University of Western Sydney, Richmond, NSW, Australia

(*Author for correspondence: tel +1 865 576 3478; email labbejj@ornl.gov)

References

- Dong S, Stam R, Cano LM, Song J, Sklenar J, Yoshida K, Bozkurt TO, Olivia R, Liu Z, Tian M *et al.* 2014. Effector specialization in a lineage of the Irish potato famine pathogen. *Science* 343: 552–555.
- Martin F, Cullen D, Hibbett D, Pisabarro A, Spatafora JW, Baker SE, Grigoriou IV. 2011. Sequencing the fungal tree of life. *New Phytologist* 190: 818–821.
- Nygren K, Strandberg R, Wallberg A, Nabholz B, Gustafsson T, García D, Cano J, Guarro J, Johannesson H. 2011. A comprehensive phylogeny of *Neurospora* reveals a link between reproductive mode and molecular evolution in fungi. *Molecular Phylogenetics and Evolution* 59: 649–663.
- Rouxel T, Grandaubert J, Hane JK, Hoede C, van de Wouw AP, Couloux A, Dominguez V, Anthouard V, Bally P, Bourras S *et al.* 2011. Effector diversification within compartments of the *Leptosphaeria maculans* genome affected by Repeat-Induced Point mutations. *Nature Communications* 2: 202.
- Soyer JL, El Ghalid M, Glaser N, Ollivier B, Linglin J, Grandaubert J, Balesdent MH, Connolly LR, Freitag M, Rouxel T, Fuda I. 2014. Epigenetic control of effector gene expression in the plant pathogenic fungus *Leptosphaeria maculans*. *PLoS Genetics* 10: e1004227.
- Tanaka S, Brefort T, Neidig N, Djamei A, Kahnt J, Vermerris W, Koenig S, Feussner K, Feussner I, Kahmann R. 2014. A secreted *Ustilago maydis* effector promotes virulence by targeting anthocyanin biosynthesis in maize. *eLife* 3: e01355.
- Veneault-Fourrey C, Martin F. 2011. Mutualistic interactions on a knife-edge between saprotrophy and pathogenesis. *Current Opinion in Plant Biology* 14: 444–450.

Key words: effectors, fungal evolution, fungal genetics and genomics, mycorrhizal fungi, pathogenic and mutualistic interactions, saprotrophs, symbiosis.

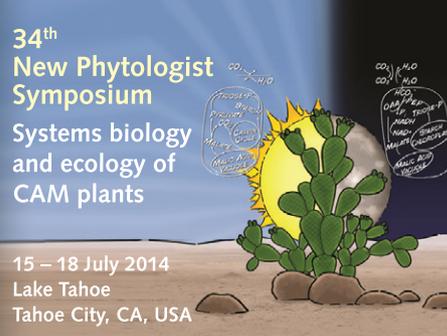
New Phytologist

Symposia for 2014

www.newphytologist.org/symposia



33rd New Phytologist Symposium
Networks of Power and Influence: ecology and evolution of symbioses between plants and mycorrhizal fungi
 14 – 16 May 2014
 Agroscope, Zurich, Switzerland



34th New Phytologist Symposium
Systems biology and ecology of CAM plants
 15 – 18 July 2014
 Lake Tahoe
 Tahoe City, CA, USA



A special event for researchers in the early stages of their careers

New Phytologist
next generation scientists

29 – 30 July 2014
John Innes Conference Centre, Norwich UK