Special issue: *Trichoderma* – from Basic Biology to Biotechnology

Gary E. Harman,¹ Alfredo H. Herrera-Estrella,² Benjamin A. Horwitz³ and Matteo Lorito⁴

Correspondence

Benjamin A. Horwitz
horwitz@tx.technion.ac.il

¹Department of Horticultural Sciences, Cornell University, Geneva, NY 14456, USA

²National Laboratory of Genomics for Biodiversity, CINVESTAV, Irapuato, Mexico

³Department of Biology, Technion, Haifa 32000, Israel

⁴Dipartimento di Arboricoltura, Botanica e Patologia Vegetale (ArBoPaVe), Università di Napoli Federico II, Portici, Napoli, Italy

Members of the genus *Trichoderma* (where known, the teleomorphs belong to *Hypocrea*) are Sordariomycetes, like the model filamentous fungus *Neurospora crassa*. *Trichoderma*'s variations on the *Neurospora* themes of morphogenesis and photobiology have been studied for several decades, pointing to those molecular details that are conserved and those that vary between species. A compelling reason to study this group is that several species are promising agents for the biocontrol of plant pathogens. In addition, the non-biocontrol agent *Trichoderma reesei* is a biotechnological factory for the production of secreted cellulases, and a model for basic studies on protein secretion (see Peterson & Nevalainen, 2012; Saloheimo & Pakula, 2012).

Although *Trichoderma* species have been considered soil inhabitants, based on *in situ* diversity studies using a taxon-specific metagenomic approach, Friedl & Druzhinina (2012) suggest that only a relatively small number are adapted to soil as a habitat. Properly selected strains interact with the plant by colonizing roots, establishing chemical communication and systemically altering the expression of numerous plant genes. Relatively recently, *Trichoderma* isolates have been identified as being able to act as endophytic plant symbionts. The strains become endophytic in roots, but the greatest changes in gene expression occur in shoots. These changes alter plant physiology and may result in the improvement of abiotic stress resistance, nitrogen fertilizer uptake, resistance to pathogens and photosynthetic efficiency. Typically, the net result of these effects is an increase in plant growth and productivity (see review by Hermosa *et al.*, 2012). A small secreted cysteine-rich protein, QID74, modifies root architecture to increase surface area (Samolski *et al.*, 2012), providing a suggestion for one of the mechanisms underlying the *Trichoderma*–root symbiosis. Therefore, regular use of *Trichoderma* spp. can help improve food security because of the reduced need to use pesticides and can provide an economic advantage for farmers. Several

papers in this issue address the *Trichoderma*–plant interaction (Ryder *et al.*, 2012; Brotman *et al.*, 2012; Rubio *et al.*, 2012). The work of 30 years of strain improvement, as part of the history of utilization of *Trichoderma* in cellulose degradation for this purpose and for the production of heterologous proteins (see Peterson & Nevalainen, 2012; Saloheimo & Pakula, 2012), is included in this issue. A series of studies has reported the use of high-throughput sequencing in gene expression analysis leading to the discovery of genes controlling asexual reproduction in response to different environmental cues (Carreras-Villaseñor *et al.*, 2012) and of genes involved in the *Trichoderma*–host interaction. Lysis of the prey's cell wall is one of the key steps during mycoparasitism. The genome analysis of two mycoparasitic *Trichoderma* species, *T. atroviride* and *T. virens*, revealed an expanded arsenal of genes encoding enzymes potentially involved in cell wall hydrolysis. It has always been puzzling how *Trichoderma* differentiates between self and non-self fungal cell wall degradation. This key question is nicely addressed by Gruber & Seidl-Seiboth (2012). Mukherjee *et al.* (2012b) review the genes which determine the secondary metabolite repertoire of *Trichoderma*, including both useful and toxic compounds, known and novel. Polyketide synthases and non-ribosomal peptide synthases (NRPSs) define two major classes of secondary metabolites (Baker *et al.*, 2012; Mukherjee *et al.*, 2012a). Peptaibols (made by NRPSs) belong to the antifungal arsenal of *Trichoderma*, and have now been found (Shi *et al.*, 2012) to trigger apoptotic death of the host.

Omann *et al.* (2012) present data in this issue about the involvement of G-protein coupled receptors in the signalling networks that control changes in gene expression. Conserved signalling pathways like this one may be critical to interactions in the soil, and the receptors, elusive until the genomes were available, provide new input to work aimed at unravelling the pathways. Other current research issues include the molecular cross-talk occurring between different mechanisms of plant disease resistance

induced by the fungi and the influence of soil biotic factors on the ecology of *Trichoderma* biocontrol agents. *Trichoderma* inoculation or infection by *Pseudomonas syringae* has been shown to have significant effects on the transcriptome and metabolome of *Arabidopsis* (Brotman *et al.*, 2012) and has been reported to affect the expression of chitinolytic enzyme-encoding genes in maize. In this issue, Matarese *et al.* (2012) present developments in strain selection, effectiveness and the mechanism of action of *Trichoderma* to control *Fusarium* head blight.

International meetings devoted to *Trichoderma* are held every 2 years; most recently a BARD (US–Israel Binational Research and Development Fund) workshop, ‘Molecular mechanisms and applications of biocontrol in agriculture’, was held at the Technion, Israel Institute of Technology, Haifa, Israel, in October 2010. The workshop took place shortly after the release of the sequenced genomes of *T. atroviride* and *T. virens*, which, together with *T. reesei*, gave novel insight into the evolution of mycoparasitism (Kubicek *et al.*, 2011). The *Trichoderma* workshop concluded with an open discussion which highlighted the importance of combining the actual knowledge, understanding and application of *Trichoderma*, including the identification of new opportunities for the exploitation of this organism’s impressive genetic potential. This special issue brings together some of the advances presented at the workshop, other recent work from the *Trichoderma* research community and a collection of reviews that will hopefully stimulate new work on this fascinating group of fungi.

REFERENCES

- Baker, S. E., Perrone, G., Richardson, N. M., Gallo, A. & Kubicek, C. P. (2012). Phylogenetic analysis and evolution of polyketide synthase-encoding genes in *Trichoderma*. *Microbiology* **158**, 147–154.
- Brotman, Y., Lisec, J., Méret, M., Chet, I., Willmitzer, L. & Viterbo, A. (2012). Transcript and metabolite analysis of the *Trichoderma*-induced systemic resistance response to *Pseudomonas syringae* in *Arabidopsis thaliana*. *Microbiology* **158**, 139–146.
- Carreras-Villaseñor, N., Sánchez-Arreguin, A. & Herrera-Estrella, A. H. (2012). *Trichoderma*: sensing the environment for survival and dispersal. *Microbiology* **158**, 3–16.
- Friedl, M. A. & Druzhinina, I. S. (2012). Taxon-specific metagenomics of *Trichoderma* reveals a narrow community of opportunistic species that regulate each other’s development. *Microbiology* **158**, 69–83.
- Gruber, S. & Seidl-Seiboth, V. (2012). Self versus non-self: fungal cell wall degradation in *Trichoderma*. *Microbiology* **158**, 9–26.
- Hermosa, R., Viterbo, A., Chet, I. & Monte, E. (2012). Plant-beneficial effects of *Trichoderma* and of its genes. *Microbiology* **158**, 17–25.
- Kubicek, C. P., Herrera-Estrella, A., Seidl-Seiboth, V., Martinez, D. A., Druzhinina, I. S., Thon, M., Zeilinger, S., Casas-Flores, S., Horwitz, B. A. & other authors (2011). Comparative genome sequence analysis underscores mycoparasitism as the ancestral life style of *Trichoderma*. *Genome Biol* **12**, R40.
- Matarese, F., Sarrocco, S., Gruber, S., Seidl-Seiboth, V. & Vannacci, G. (2012). Biocontrol of *Fusarium* head blight: interactions between *Trichoderma* and mycotoxigenic *Fusarium*. *Microbiology* **158**, 98–106.
- Mukherjee, P. K., Horwitz, B. A. & Kenerley, C. M. (2012a). Secondary metabolism in *Trichoderma* – a genomic perspective. *Microbiology* **158**, 35–45.
- Mukherjee, P. K., Buensanteai, N., Moran-Diez, M. E., Druzhinina, I. S. & Kenerley, C. M. (2012b). Functional analysis of non-ribosomal peptide synthetases (NRPSs) in *Trichoderma virens* reveals a polyketide synthase (PKS)/NRPS hybrid enzyme involved in the induced systemic resistance response in maize. *Microbiology* **158**, 155–165.
- Omann, M. R., Lehner, S., Escobar Rodriguez, C., Brunner, K. & Zeilinger, S. (2012). The seven-transmembrane receptor Gpr1 governs processes relevant for the antagonistic interaction of *Trichoderma atroviride* with its host. *Microbiology* **158**, 107–118.
- Peterson, R. & Nevalainen, H. (2012). *Trichoderma reesei* RUT-C30 – thirty years of strain improvement. *Microbiology* **158**, 58–68.
- Rubio, M. B., Domínguez, S., Monte, E. & Hermosa, R. (2012). Comparative study of *Trichoderma* gene expression in interactions with tomato plants using high-density oligonucleotide microarrays. *Microbiology* **158**, 119–128.
- Ryder, L. S., Harris, B. D., Soanes, D. M., Kershaw, M. J., Talbot, N. J. & Thornton, C. R. (2012). Saprotrophic competitiveness and biocontrol fitness of a genetically modified strain of the plant-growth-promoting fungus *Trichoderma hamatum* GD12. *Microbiology* **158**, 84–97.
- Saloheimo, M. & Pakula, T. M. (2012). The cargo and the transport system: secreted proteins and protein secretion in *Trichoderma reesei* (*Hypocrea jecorina*). *Microbiology* **158**, 46–57.
- Samolski, I., Rincón, A. M., Pinzón, L. M., Viterbo, A. & Monte, E. (2012). The *gid74* gene from *Trichoderma harzianum* has a role in root architecture and plant biofertilization. *Microbiology* **158**, 129–138.
- Shi, M., Chen, L., Wang, X.-W., Zhang, T., Zhao, P.-B., Song, X.-Y., Sun, C.-Y., Chen, X.-L., Zhou, B.-C. & Zhang, Y.-Z. (2012). Antimicrobial peptaibols from *Trichoderma pseudokoningii* induce programmed cell death in plant fungal pathogens. *Microbiology* **158**, 166–175.