seems to inspire great science. Since moving, I've developed wonderful long-term collaborations with my colleagues Phil Zamore and Zhiping Weng. I love to think about the biology of germline development; Phil has amazing insights into small RNA function and mechanism; and Zhiping can pull it all together through elegant and rigorous computational analyses. Working with these two has been a blast, and I can honestly say that I'm more excited than ever about the science we're doing.

Do you have a scientific hero? Yes: Bruce Alberts. I was a postdoc in Bruce's lab, and it was a fantastic experience. He is very creative and encouraged risk taking and independence. Everyone in the lab was energized by his enthusiasm for science. Bruce's intellectual honesty and integrity also impressed me, and I think these traits are one reason he's so widely respected. He was a great scientific mentor, but he also taught me to reach beyond the bench and into the community. He founded the Science Education Partnership at USCF, which pairs grad students and postdocs with teachers in local schools. As a postdoc, I worked with a middle school teacher on meiosis and mitosis labs and mentored a high school student, which were great experiences. Outreach programs are clearly good for science education, but it also connects the public with science, which may be even more important. Our work has become increasingly politicized, and the public pays for most of what we do. If scientists want politicians to make informed decisions on issues ranging from stem cell research to the NIH budget, they need to help the public understand and feel connected to science. The best way to do this is through the schools. Bruce was clearly a pioneer in educational outreach, and this is more important than ever.

What is your greatest ambition? Science is a process, not an end point, so I don't really have a specific goal or discovery I'd like to make. My main ambition is to remain open-minded and help push the process along.

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Quick guide

Trichoderma

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***What is* Trichoderma?** The genus *Trichoderma* comprises a large number of rhizocompetent filamentous fungal strains found in a large variety of ecosystems. These fungi are mostly isolated from forest or agricultural soils at all latitudes and can be easily cultured *in vitro*. They present a typical green sporulation (Figure 1) and some species produce a characteristic sweet or 'coconut' odor due to a biologically active volatile compound (6-pentyl-α-pyrone). The mycoparasitic nature (the ability to attack other fungi and utilize their nutrients) of *Trichoderma* and their potential use as biocontrol agents of plant pathogenic fungi has been known for more then six decades. During this period, several strains of *Trichoderma*, some of which are also opportunistic plant symbionts, have been developed as biocontrol agents against plant diseases, while others such as *Trichoderma reesei* are industrially important cellulolytic filamentous fungi.

Why use* Trichoderma *as plant biocontrol agents? Biological control, the use of specific organisms that interfere with plant pathogens and pests, is a nature-friendly, ecological approach to overcome the problems caused by standard chemical methods of plant protection. Modern agriculture is highly dependent on the use of chemical pesticides to control plant pathogens. Growing awareness of the environmental damage caused by the use of chemical substances for plant disease control in agriculture has motivated the study of biological alternatives. One of the key concerns in this approach is the question of specificity of the biological control agent released in a new ecosystem, and the feasibility of such introductions need therefore to be carefully assessed. However, this should not be a major concern since *Trichoderma* fungi are widespread in most ecosystems.

The antagonistic properties of *Trichoderma* spp. towards fungal pathogens are based on the activation of multiple mechanisms that include competition for nutrients and space, mycoparasitism, antibiosis, promotion of plant growth and plant defense responses.

How do* Trichoderma *spp. attack plant pathogens? Mycoparasitism appears to be a complex process and depends on a combination of mechanisms acting sequentially or together. *Trichoderma* is a strong mycoparasite; it is attracted to

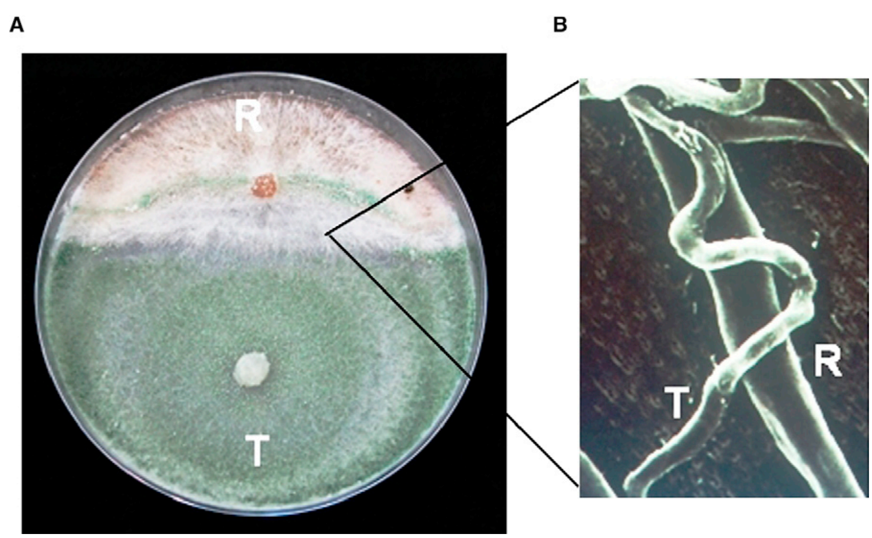

Figure 1. *Trichoderma* mycoparasitism.
(A) Mycoparasitic confrontation assay and (B) coiling of *Trichoderma* (T) hyphae around the plant pathogen *Rhizoctonia solani* (R).

Figure 2. Growth promotion effect of *Trichoderma* (T) on cucumber seedlings.

and grows towards its host (plant pathogen) probably by chemotropism. Host signals may act at a distance without physical contact, and some of these signals may be released from the host by the action of the cell-wall degrading enzymes made by the *Trichoderma*. Upon contact with the host (apparently mediated by a lectin-specific interaction), *Trichoderma* coils around (Figure 1) or grows along the host hyphae and forms hook-like structures that aid in penetrating the host's cell wall. Penetration thus seems to occur both mechanically and enzymatically by secretion of an array of cell-wall degrading enzymes, including powerful chitinases. Antibiotic production is considered to play an important role during biocontrol events. Different volatile and nonvolatile secondary metabolites have also been characterized from *Trichoderma* spp. with high antimicrobial and plant defense inducing activities.

How do* Trichoderma *spp. interact with plants? Some rhizosphere-competent strains of *Trichoderma* can colonize entire root surfaces with morphological features reminiscent of those seen during mycoparasitism and can be defined as opportunistic plant symbionts. Penetration of the root tissue is usually limited to the first or second layers of cells and only to the intercellular spaces. Hydrophobin proteins are involved in early attachment to root surfaces. Swollenin, an expansin-like protein, is involved in the loosening of the plant cell wall by expanding cellulose fibers, thus facilitating the action of a vast arsenal of cell-wall degrading cellulases. *Trichoderma* strains capable of establishing such interactions induce massive changes in the plant transcriptome and metabolism that lead to the accumulation of antimicrobial compounds affording resistance to a wide range of plant-pathogenic microorganisms. This response seems to be broadly effective for many plants, which indicates that there is little or no plant specificity. Elicitors of plant defense responses include small peptides, proteins, protein domains and low molecular-weight compounds from fungal or plant cell wall origin, including products of fungal enzymatic lytic degradation.

What's the benefit for the plant? Like beneficial plant rhizobacteria, *Trichoderma* can induce priming for enhanced defense in plants. In primed plants, defense responses are not activated directly by the beneficial microorganism but are accelerated upon pathogen or insect attack, resulting in enhanced resistance to the attacker.

Priming is one of the most economical and effective modes of resistance because it prevents wasteful metabolic consumption in plants. The fitness costs of priming are lower than those of constitutively activated defenses, suggesting that priming functions as an ecological adaptation of the plant to respond faster to a hostile environment. Moreover, many *Trichoderma* species are able to promote plant growth and development (Figure 2). There have been reports that *Trichoderma* can promote plant growth up to 300%. The growth promotion seems to be mediated by auxin production by the fungus and by fungal 1-Aminocyclopropane-1-carboxylate deaminase activity, which lowers high levels of ethylene that accumulate during various stresses. *Trichoderma* spp. also produce organic acids such as gluconic, fumaric and citric acids that can decrease soil pH and allow solubilization of phosphates, as well as micro- and macro-nutrients such as iron, manganese and magnesium that are vital for plant metabolism. In addition, the ability of *Trichoderma* strains to induce greater root systems and enhance plant health provides more niches for growth of the fungus.

What is the relevance to agriculture and industry? Around 50 different *Trichoderma*-based agricultural formulations can be found as registered products in various countries and are applied to protect and improve the yields of vegetable, ornamental and fruit plantations. These beneficial fungi are among the most resistant microbes to natural and synthetic chemicals and toxins, and are able to rapidly degrade some of them. As such, *Trichoderma* strains play an important role in the bioremediation of contaminated soils and can be applied in integrated pest management and phytoremediation. Variability in performance in different ecosystems still limits wider use of these fungi in biocontrol. Moreover, in order to enhance marketability of these fungi, feasible commercial production processes are of utmost importance. Currently, the high cost of raw materials used in culture media for production, low spore yield, and difficulties in quantification of biocontrol activity all constrain commercialization of *Trichoderma* spp. On the industrial front, *T. reesei*, a cellulolytic producer strain, is currently used as a host to produce low cost enzymes for the conversion of plant biomass materials into industrially useful biproducts, such as sugars and bioethanol.

Where can I learn more?

Alfano, G., Lewis Ivey, M.L., Cakir, C., Bos, J.I.B., Miller, S.A., Madden, L.V., Kamoun, S., and Hoitink, H.A.J. (2007). Systemic modulation of gene expression in tomato by *Trichoderma hamatum* 382. Phytopathology *97*, 429–437.

Dashtban, M., Schraft, H., and Qin, W. (2009). Fungal bioconversion of lignocellulosic residues; opportunities and perspectives. Int. J. Biol. Sci. *5*, 578–595.

Harman, G.E., Howell, C.R., Viterbo, A., Chet, I., and Lorito, M. (2004). *Trichoderma* spp.: opportunistic avirulent plant symbionts. Nat. Microbiol. Rev. *2*, 43–56.

Segarra, G., Van der Ent, S., Trillas, I., and Pieterse, C.M. (2009). MYB72, a node of convergence in induced systemic resistance triggered by a fungal and a bacterial beneficial microbe. Plant Biol. *11*, 90–96.

Shoresh, M., Harman, G.E., and Mastouri, F. (2010). Induced systemic resistance and plant responses to fungal biocontrol agents. Annu. Rev. Phytopathol. *48*, *Reviews in Advance*.

Vinale, F., Sivasithamparam, K., Ghisalberti, S., and Lorito, M. (2008). *Trichoderma*–plant–pathogen interactions. Soil Biol. Biochem. *40*, 1–10.

Vinale, F., Flematti, G., Sivasithamparam, K., Lorito, M., Marra, R., Skelton, B.W., and Ghisalberti, E.L. (2009). Harzianic acid, an antifungal and plant growth promoting metabolite from *Trichoderma harzianum*. J. Nat. Prod. *72*, 2032–2035.

Viterbo, A., and Horwitz, B. (2010). Mycoparasitism. In Cellular and Molecular Biology of Filamentous Fungi. K. Borkovich and D. Ebbole, eds. (ASM Press), pp. 676–693.

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