

## CHANGING PARADIGMS ON THE MODE OF ACTION AND USES OF *TRICHODERMA* SPP. FOR BIOCONTROL

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*Trichoderma* spp. have been known to control plant diseases biologically for more than 70 years (Weindling, 1932; Weindling & Fawcett, 1936). Within the past decade, these fungi have begun to be used widely in commercial agriculture (Harman, 2000). The long period of development between the original discoveries of some of the useful properties of these fungi and their first commercial adoption can be explained in part by an incomplete understanding of the nature of the biocontrol interaction.

As recently as the 1990s, the ability of these fungi to control plant diseases was attributed in large part to their direct effects on other fungi, especially their abilities to function as parasites of plant pathogenic fungi and to produce antibiotics (Chet *et al.*, 1998; Harman & Kubicek, 1998; Howell, 1998). These are real phenomena and occur in nature. However, disease biocontrol may be more closely associated with the ability to compete with pathogens in soil than with their direct ability to control plant diseases. The fungi efficiently induce systemic resistance, as has been demonstrated in both axenic and field soil systems on a wide range of plant/pathogen combinations (Geremia *et al.*, 1993; Harman *et al.*, 2004a; Yedidia *et al.*, 1999; Yedidia *et al.*, 2000; Yedidia *et al.*, 2003). If this is so, then efforts to select improved strains based on parasitism and antibiosis were flawed since they were not selecting for the appropriate characteristics.

In addition to biocontrol capabilities, these fungi also have other direct effects on plants. These include the following:

- Increased growth and yields of plants (Chang *et al.*, 1986; Harman, 2000; Lindsey & Baker, 1967; Yedidia *et al.*, 2001)
- Increased root growth and drought tolerance (Harman, 2000)
- Induced systemic resistance to disease (Geremia *et al.*, 1993; Harman *et al.*, 2004a; Yedidia *et al.*, 1999; Yedidia *et al.*, 2000; Yedidia *et al.*, 2003)
- Increased nutrient uptake and fertilizer efficiency utilization (Harman, 2000, 2001; Yedidia *et al.*, 2001)
- Increased leaf greenness that is probably related to increased photosynthetic rate (Harman, 2000; Harman & Shores, 2007)
- Increased percentages of germination and rates of germination of seeds (Björkman *et al.*, 1998; Chang *et al.*, 1986)

### Advantages of *Trichoderma* biocontrol systems over chemical control methods

In some cases, the beneficial effects on plants are very long lasting. This can occur because the *Trichoderma* spp. set up symbiotic interactions with plants and, like other root colonizing microbes such as rhizobia and mycorrhizae, these interactions continue for an extended time. The best strains are able to grow with the plant roots and provide season-long benefits. For example, a seed treatment of maize with *Trichoderma harzianum* strain T22 resulted in (a) greater growth and yield of the final crop, (b) greater leaf greenness, (c) rooting that was about twice as deep in the mature plant and (d) greater efficacy of use of nitrogen fertilizer (Harman, 2000, 2001). This season long beneficial effect of *Trichoderma* seed inoculants on plant productivity occurs because T22 is strongly rhizosphere competent and persists as a root symbiont over a long period of time.

### Control of Foliar Diseases without Fungicide Applications

Soil or seed inoculation can result in whole plants that are systemically induced to be resistant to a variety of plant pathogens. As a consequence, disease control of foliar diseases can probably be accomplished by application of biocontrol *Trichoderma* spp. only to soil, with the biocontrol organism colonizing only the roots. This effect has been demonstrated with both *Trichoderma* spp. and bacteria. Induced systemic resistance requires initial triggering by a specific molecule, followed by a cascade of changes within the plant. It is important to emphasize that the biocontrol agent, therefore, is not controlling disease by producing something toxic to the pathogen, but it is instead inducing the plant to change its physiology and metabolism to produce resistance metabolites.

Further, it is important to note that some strains are endophytes, i.e., they colonize not only roots, but also the above-ground parts of plants. These are being investigated for control of tropical tree diseases, such as those affecting cacao (Bailey *et al.*, 2006). These endophytes provide another avenue for potential biocontrol systems using *Trichoderma* spp., together with additional opportunities for study of these novel plant-microbe interactions. It is not known at this time whether endophytic and root-colonizing abilities are separate phenomena, or if strains that are strongly competent in one trait may also possess the other.

To summarize, *Trichoderma* spp. induce systemic resistance to plant diseases. These systems have significant

potential advantages for plant disease control. First, it provides opportunities for control of diseases without actual foliar sprays. This reduces environmental consequences of pesticide applications and saves users money. Second, the effects may be long lasting; T22 added to tomato transplants at the start of the season resulted in plants that were substantially less susceptible to the foliar disease early blight several months later (Harman *et al.*, 2004a). Finally, the range of pathogens controlled may be quite large and may include fungi, bacteria and even a virus (Harman *et al.*, 2004a). The control of foliar diseases by soil or seed applications of *Trichoderma* and other biocontrol organisms is just beginning.

## The mechanisms and systems by which *Trichoderma* induces resistance

There are two pathways of induced resistance in plants: systemic acquired resistance mediated by salicylic acid (SA pathway), and induced systemic resistance, mediated by jasmonic acid and ethylene (JA/Et pathway). While both pathways have been relatively well described in dicotyledons, the existence of similar pathways in monocotyledons has not been well documented. The first to document the induction of the JA/Et pathway by *Trichoderma* spp. in a monocot used *T. virens* to induce resistance in maize (Djonovic *et al.*, 2007). Efficient methods to induce resistance in monocots have not been available, but *Trichoderma*-plant interactions may provide the necessary tool to examine these pathways in detail.

*Trichoderma* spp. have many effects on plant physiology, making it challenging to isolate the interactions associated with triggering plant resistance. Nevertheless, the international *Trichoderma* research community has a consensus on the events that occur in the *Trichoderma*-plant interaction (Harman *et al.*, 2004a). These events can be summarized as follows:

- *Trichoderma* strains colonize and infect the outer layers of roots (Yedidia *et al.*, 1999; Yedidia *et al.*, 2000).
- Once infection occurs, a zone of chemical interaction develops at these sites. Within this zone of chemical interaction, the *Trichoderma* hyphae are walled off by the plant but are not killed (Harman *et al.*, 2004a; Harman & Shoresh, 2007).
- Chemical elicitors from *Trichoderma* produced by the walled off hyphae interact with putative plant receptors (Harman *et al.*, 2004a; Harman & Shoresh, 2007).

Thus, if a strain is highly rhizosphere competent, then the next important component is the signaling molecules that the fungi produce. Different strains produce different molecules, and this variation determines the outcome of the reaction. Therefore, if the signaling molecules change, then the plant-microbe outcome will be altered. This is indeed true; causing *T. atroviride* or *T. harzianum* to secrete glucose oxidase increases biocontrol efficacy (Brunner *et al.*, 2005), which is likely to result from induction of the SA pathway. As noted later, other strains and their elicitors induce the JA/Et pathway. It is likely that expression of glucose oxidase alters the pathways of induced resistance that are expressed.

There are a number of elicitors that have been identified in *Trichoderma* spp. One of these, a small hydrophobin-like molecule, Sm1, induces the JA/Et pathway. It must be present for resistance to disease to be induced by some strains of *T. virens* in both cotton and maize (Djonovic *et al.*, 2006; Djonovic *et al.*, 2007).

Another novel hydrophobin was found to be produced by T22 (Ruocco *et al.*, 2007). Hydrophobins are a class of small cystein-rich proteins that are expressed only by fungi. Some years ago, we noted qualitatively similar responses by preparations of T22. Dipping the cut ends of tomato stems in powders containing T22 induced rooting more effectively than rooting hormones (Fig. 1), but the reaction that occurred was different. Rooting hormones resulted in callus formation on the end of the stem, while no such reaction occurred with T22. The new roots developed from the callus, while in T22-treated plants, a fringe of roots initially developed around the periphery of the cut stems. In addition, micropropagation of apple explants routinely uses T22 to aid rooting (Bolar *et al.*, 1998). One effect that many *Trichoderma* strains induce is enhanced root development – is the hydrophobin the necessary triggering molecule for this reaction? If so, this is a significant discovery with considerable commercial value. The T22 hydrophobin also induces resistance as well as rooting (Ruocco *et al.*, 2007), but it is a different molecule than Sm1. Other elicitors may or may not induce multiple beneficial responses in plants. Tests are planned that will directly compare the effects of the pure hydrophobin and T22, and then reverse genetic engineering approaches are planned to determine specifically whether this molecule is sufficient to cause both enhanced rooting and induced resistance.

In many respects, the interaction of *T. virens* with maize and cotton, where the JA/Et pathway of resistance is induced, is similar to another host-*Trichoderma* combination, *T. asperellum* and cucumbers. There, it is again the JA/Et pathway that is induced (Shoresh *et al.*, 2005). In this case, it is known that after the reaction occurs, the signal for induced resistance is transduced through a specific protein MAP

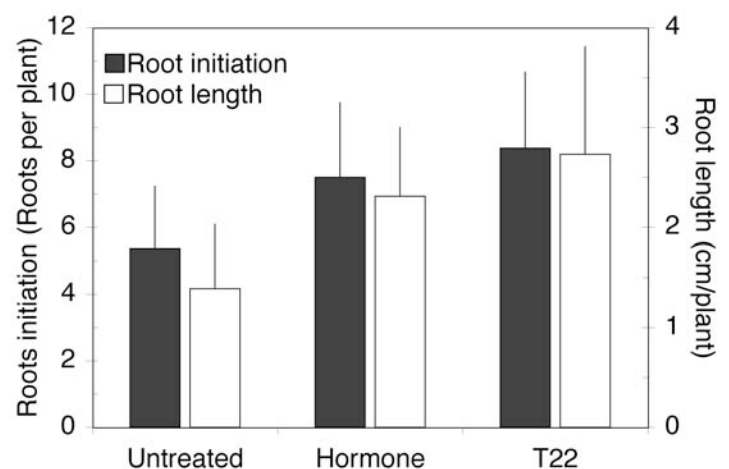


Figure 1. Rooting initiation and growth of cutting of a *Solanum X Lycopersicon* hybrid after 13 days. Cut ends of stems were untreated, treated with commercial rooting hormone, or treated with powders of T22. The values shown are the means from 8 replicates (separate plants) for each treatment and the bars indicate standard deviations around the mean.

kinase. If this plant protein is silenced, then no induced resistance occurs; if it is constitutively overexpressed, then the plants become resistant to disease even in the absence of *T. asperellum* (Shoresh *et al.*, 2005). Thus, it is evident that not only do *Trichoderma* spp. induce resistance, but that study of them can result in improved knowledge of the pathways of resistance in plants. However, it is likely that, by changing the elicitor molecules, we can alter both the level and pathway that is induced. It is postulated that the ability of glucose oxidase to increase the level of resistance may occur because it fosters the induction of the SA pathway, so that both the JA/Et and the SA pathways may be induced at the same time.

Thus, strains that are highly capable of colonizing roots, and establishing symbiotic infections in plant roots, can be viewed as delivery vehicles for different signaling molecules, the elicitors, into plant cells. Any given strain may produce a mixture of different elicitors and this mixture appears to determine the nature and efficacy of the plant-microbe interaction. This hypothesis will be tested.

### Changes in the plant induced by *Trichoderma* spp.

The numerous benefits of these fungi on plant growth and resistance must be reflected in changes in the physiology of plants. The proteome and transcriptome of plants changes as a consequence of *Trichoderma* metabolites (Marra *et al.*, 2006) or plant colonization (Alfano *et al.*, 2007; Harman & Shoresh, 2007). In the latter two studies, *Trichoderma* strains were present only on roots and the effects were systemic throughout the plant. In our work, the presence of *T. harzianum* strain T22 on roots up-regulated 114 maize proteins and down-regulated 50 proteins. Of these, 121 were identified. The largest number of up-regulated proteins was involved in carbohydrate metabolism, with substantial increases in proteins involved in photosynthesis, as well as disease and stress resistance. Colonization of tomato roots by *Trichoderma hamatum* caused a change in the transcript abundance of 45 shoot genes. As in maize, genes associated with stress or defense functions were among the most frequently changed, along with genes associated with RNA, DNA or protein metabolism (Alfano *et al.*, 2007). However, energy metabolism (photosynthesis and carbohydrate metabolism) was less affected. In cacao trees infected with several endophytic *Trichoderma* strains, genes involved with plant stress resistance were consistently up-regulated (Bailey *et al.*, 2006), though there was variation in the specific genes up-regulated in the presence of different strains.

Genes supporting more rapid growth appear to be up-regulated. In maize, increased capacity for photosynthesis and primary carbohydrate metabolism can support greater growth (Harman & Shoresh, 2007). In addition, proteins that determine the rate of cell enlargement are up-regulated. In the maize-T22, the tomato-*T. hamatum* and the endophyte-cacao systems, genes encoding cell wall-related proteins (expansins and/or extensins) were up-regulated (Harman, unpublished; Alfano *et al.*, 2007; Bailey *et al.*, 2006). These proteins are involved in cellular

expansion and growth and may be consequences of the plant growth-promoting abilities of these organisms.

These studies indicate that the changes in plant physiology by root colonization by *Trichoderma* spp. are indeed large. The demonstration that genes and proteins involved in plant disease resistance, respiration and photosynthesis are up-regulated in the presence of T22 begins to explain the effects of this fungus noted at the beginning of this article.

Thus, the changes induced in gene and protein expression are fully consistent with the concept of large changes induced by *Trichoderma* spp. in plant physiology and function. These fungi provide an important new tool to understand plant responses and to manipulate them to increase yield and crop productivity. Resistance-inducing biocontrol fungi can also be powerful tools to improve plant agriculture.

### Commercial implications

There are two basic methods by which this mechanistic information can be used to improve commercial biocontrol. The first is based upon a concept of 'molecular signatures' that indicate highly successful biocontrol. Thus, the basic information just described can be used to identify specific plant genes that are activated in, or gene products that are indicative of, very successful biocontrol/plant growth promotive associations. These signatures, when the research is complete, can be relatively simple and can be used for (a) screening of new strain/plant combinations or specific plant varietal interactions, and (b) direct monitoring of activity of the strains in growing plants, even in the field. For (a), a set of critical genes or gene products will be identified and specific, rapid tests will be developed for them. These then can be used much more precisely and rapidly than plant disease control or plant growth assays to evaluate plant responses. However, results of the molecular tests will still need to be verified by direct measurement of effects on plants. For (b) the same platform of tests can be used either in the laboratory or in the field. Rapid, portable equipment and procedures are being developed so that techniques such as quantitative PCR, which measures the expression of specific genes, and gas chromatographic/mass spectrometry equipment for identification of plant metabolites, are becoming available. Thus, it ought to be possible soon to assess the ability of the beneficial microbes in plants in the field to induce critical beneficial changes in the plant physiology that are not normally present in the absence of the beneficial microbes. This can be used for physiological tests for academic study or even for companies that market the beneficial microbes to demonstrate to customers that indeed the expected changes are occurring. This would be a powerful marketing tool.

Beyond this, as described in the next section, we already are taking advantage of the new knowledge in screening for better biocontrol agents. Since we now know that systemic resistance is induced by root colonizing microbes, we can screen for disease resistance in the foliage. This will serve two functions – first, to discover '21<sup>st</sup> century' biocontrol agents to replace the ones in use now, and, once better strains are discovered, these can be placed back into the basic discovery



process and the precise reasons why they are better can be determined. This will increase the pool of useful organisms and increase our knowledge base that can be used in the 'molecular signatures' approaches.

## Strain selection

We were interested in selecting microbial strains that, when added to planting medium, would induce foliar resistance to plant diseases. Our standard plant-pathogen system was powdery mildew on cucumber. However, comparable resistance can be seen in other plant-pathogen combinations, such as maize-*Colletotrichum graminicola* (Harman *et al.*, 2004b), which suggests that induced resistance responses occur generally.

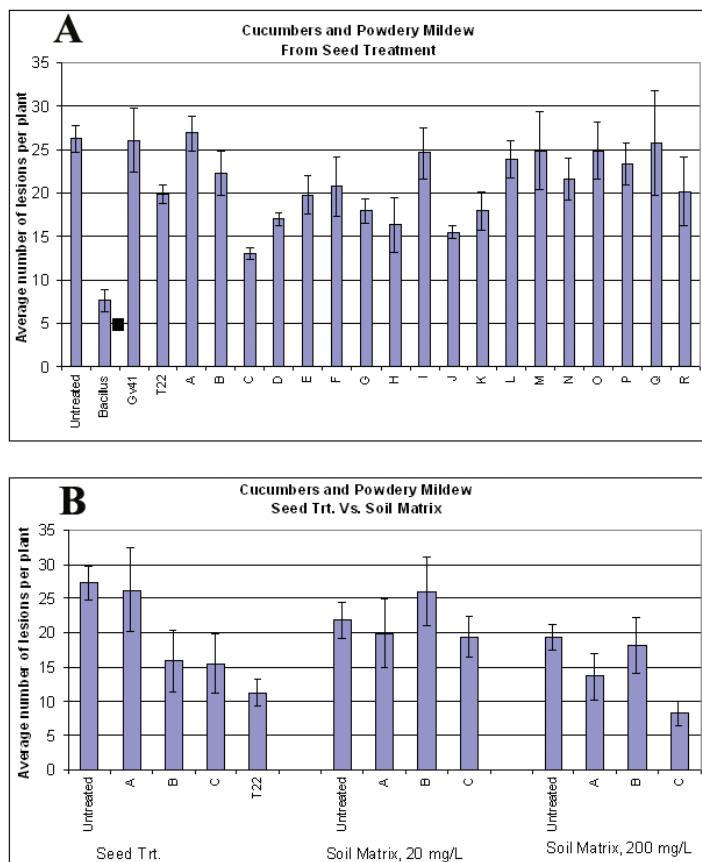


Figure 2. Effects of seed or soil treatment on induced resistance leading to control of powdery mildew on cucumber seedlings at about 21 days after planting. Seeds were treated with various strains of *Trichoderma* (Gv41, T22 and strains A-R) or *Bacillus subtilis* (A) to provide about  $5 \times 10^5$  cfu/seed. Alternatively, seeds were treated as above, or else inoculum was added to soil at the levels indicated, with a powdered inoculum of about  $10^9$  cfu/g (B). In all experiments, at about 17 days after planting, seedlings were at the 2-3 leaf stage. Spores of the cucumber powdery mildew pathogen *Podosphaera (Sphaerotheca) xanthii* were removed from infected leaves by spraying. The inoculum was adjusted to  $1-5 \times 10^5$  spores/ml and sprayed to run-off using a spray bottle. The plants were grown with at least 60% humidity so that pathogen infection could occur. About 7-10 days after inoculation, disease incidence was evaluated and expressed as numbers of lesions per plant. The bars represent standard errors about the mean (four plants per treatment). In (A), the black square represents the level of disease control provided by a standard fungicide.

Seeds or soil were treated with candidate strains of biocontrol organisms, allowing the roots to be colonized. The shoots were then challenged with powdery mildew. A number of *Trichoderma* strains and one strain of *Bacillus subtilis* were evaluated as seed treatments for their abilities to induce systemic resistance (Fig.2). A *B. subtilis* (Bergstrom & da Luz, 2005) was nearly as effective as some foliar fungicides, while *Trichoderma* strains C and J were protective, but to a lesser extent. Several *Trichoderma* strains were also compared as seed and soil treatments. While seed treatments are known to result in good colonization, soil treatment has been less consistent. Soil treatment increased the level of *Trichoderma* spp. from about  $10^4$  to about  $10^6$  colony forming units (cfu) per g of root. New strain C was the most effective.

These data indicate that induced resistance works, and the right strains or strain combinations provide considerable protection. This screening protocol has two valuable uses: (a) to discover strains that provide high levels of control of foliar diseases for immediate commercial uses; and (b) to identify plant-biocontrol agent combinations that are good tools to screen for the best elicitor molecules. From this latter work, we expect to be able to identify and produce progressively better strains efficiently.

We found that growth promotion is not solely a function of reduced disease. Some of the *Trichoderma* strains that were ineffective in inducing foliar disease control (Fig. 2A) nevertheless provided high growth stimulation (data not shown). This suggests that the two plant responses are in response to different *Trichoderma* elicitors.

## Limitations of Induced Resistance and Related Responses

The efficacy of defense systems induced by colonization of roots with *Trichoderma* spp. and other biocontrol organisms is likely to be commercially useful, and probably explains some of the commercial successes obtained thus far. However, the changes that occur are complex and brought about specific interactions of the biocontrol agent, together with the elicitors they produce, with the plant. While the effects occur across a range of plant species with single biocontrol agents, there are varietal responses within species. For example, *T. harzianum* strain T22 as a seed treatment on maize gave an average 5% yield increase across more than 800 field trials. However, individual inbreds and hybrids varied in their responses (Harman, 2006). Similar varietal interactions with *Trichoderma* spp. were noted with tomato (Ruocco *et al.*, 2007). In wheat the varietal effect is lower, and more than 90% of US field trials have resulted in yield increases despite a range of wheat varieties.

The resistance obtained is useful, but is short of immunity. While disease is reduced, it is not eliminated. Under conditions of severe disease pressure, some additional control measures may be needed. In addition, the resistance responses are likely to be less effective in older plants. Since the resistance pathways are dependent upon active growth and respiration, the resistance that is induced will be lower as older leaves begin to shut down.

Finally, some strains are very good at inducing increased growth responses, while others are very good at inducing resistance. *T. harzianum* T22 seems to be a good generalist.

We expect that, as the full mechanisms of the changes induced by root colonization are understood, including both the elicitors produced by effective strains as well as the changes induced in plants, it will be possible to use this knowledge to produce much more effective biocontrol organisms and systems. These developments are occurring at a rapid pace and are likely to produce markedly better biocontrol systems and practices. We hypothesize that changes in the elicitor profiles of *Trichoderma* spp. will alter the responses of plants to the fungi, and that very significant gains can be made in plant productivity and stress responses and that biocontrol can be made by manipulation of these elicitor profiles.

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