Induced Systemic Resistance and Plant Responses to Fungal Biocontrol Agents

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Local infection by non-pathogenic bacteria or fungi can induce plants to develop a plant-wide resistance against potential attack by a number of pathogens. The systemic response in plants occurs through the jasmonic acid/ethylene signalling pathways in a similar manner to the rhizobacteria induced systemic resistance. Biocontrol fungi are beneficial organisms that reduce the negative effects of plant pathogens and encourage positive responses in the plant. They do control diseases and additionally have other benefits as well.

Introduction
Contact with pathogenic and non-pathogenic microorganisms activates a broad range of defense mechanisms in plants. Two main mechanisms are recognized; systemic acquired resistance and induced systemic resistance. Biocontrol fungi (BCF) are agents that control plant diseases that comprises of Trichoderma spp. and Sebacinales spp. They comprise the ability to control several foliar, root, and fruit pathogens and nematodes. Though, this is only a subset of their abilities. BCF also augments nutrient uptake and increase nitrogen use efficiency in crop plants. Some strains also have abilities to improve photosynthetic efficiency of plants.

Induced systemic resistance
Induced systemic resistance (ISR) emerged as an important mechanism by which selected plant growth promoting bacteria (PGPR) and fungi in the rhizosphere primed the entire plants for enhanced defense against a number of plant pathogens. ISR is elicited by a local infection, plants respond with a jasmonic acid and ethylene dependent signalling cascades that lead to the systemic expression of a broad spectrum and long-term disease resistance which is effective against fungi, bacteria and viruses. ISR is the activation of latent innate immune responses. It develops systemically in response to colonization of plant root by PGPR and mycorrhizal fungi. ISR does not involve the accumulation of pathogenesis-related proteins or but instead, relies on jasmonic acid and ethylene dependent signalling pathways.

Fungal biocontrol agents
Biocontrol fungi (BCF) are beneficial organisms that reduce the harmful effects of plant pathogens and encourage positive responses in the plant. They aren’t only controlling diseases,
but also have other benefits, including amelioration of inherent physiological stresses in seeds and alleviation of abiotic stresses. They also improve photosynthetic efficiency and nitrogen use efficiency in crop plants. Use of biocontrol agents (BCAs) offers a more sustainable method of crop production as they reduce environmental impact and, therefore, increased biodiversity, because BCAs are usually more target specific than chemicals. Consequently, plants treated with beneficial fungi may be larger and healthier and have better yields than plants without them.

Mechanisms of Fungal Biocontrol Agents

1. Mycoparasitism
   It is a process by which biocontrol fungi may attack pathogenic fungi. Mycoparasitism has long been considered an important mechanism of action of biocontrol by *Trichoderma* spp. This is a complex process that involves the tropic growth of the biocontrol agent against target fungi, lectin-mediated coiling of attachment of *Trichoderma* hyphae to the pathogen, and ultimately attack and dissolution of the target fungus’ cell wall by the action of enzymes, which is associated with the physical penetration of the cell wall. The *Trichoderma* chitinase and β-1,3-glucanase involved in mycoparasitic interactions. Another mycoparasitic fungus, *Sporidesmium sclerotivorum*, parasitizes *Sclerotinia minor* and *Sclerotium cepivorum* (the causal agents of lettuce drop).

2. Antibiosis
   Antibiosis is defined as the interactions that involve a low-molecular weight compound or an antibiotic produced by a microorganism that has a direct effect on another microorganism. Most microbes produce and secrete one or more compounds with antibiotic activity. In some cases, antibiotics produced by microorganisms have been shown to be particularly effective at suppressing plant pathogens and the diseases they cause. The ability to produce many classes of antibiotics, which differentially inhibit different pathogens growth, is likely to enhance biological control. E.g. *Trichoderma virens* produced Gliotoxin which is effective against *Rhizoctonia solani*, *Chaetomium globosum* strain Cg-13 produced Chaetomin which target *Pythium ultimum* in sugar beet.

3. Competition
   To successfully colonize the phyllosphere, a microbe must effectively compete for the available nutrients. On plant surfaces, host-supplied nutrients include exudates, leachates, or senesced tissue. Generally; nutrient competition has been supposed to have an important role in disease suppression. Biocontrol by means of nutrient competition can occur when the biocontrol agent decreases the availability of a particular substance thus limiting the growth of the plant pathogenic agents. In general, soil borne pathogens, such as species of *Fusarium* and *Pythium*, which infect through mycelial contact, are more vulnerable to competition from other soil and plant associated microbes than those pathogens that germinate directly on plant surfaces and infect through appressoria and infection pegs.
4. Induction of host resistance

Plants actively react to an array of chemical stimuli produced by soil and plant associated microbes. Such stimuli can induce plant host defenses through biochemical changes that improved resistance against succeeding infection by pathogens. Stimulation of host defenses can be local and/or systemic in nature, depending on the type, source and amount of stimuli. It is of two types:

a. **Systemic acquired resistance (SAR):** This pathway is mediated by salicylic acid (SA), a compound which is often produced following pathogen infection and leads to the expression of pathogenesis-related (PR) proteins. These PR proteins include a diversity of enzymes, some of which may act directly to lyse invading cells, reinforce cell wall boundaries to oppose infections, or induce localized cell death.

b. **Induced systemic resistance (ISR):** It is defined as the resistance induced in leaves of plants by inoculation of roots with non-pathogenic rhizobacteria. It does not involve the accumulation of pathogenesis-related proteins and is mediated by jasmonic acid and/or ethylene, which are produced following applications of some non-pathogenic rhizobacteria.

5. Cross protection

It differs from induced resistance in that, subsequent inoculation with avirulent strains of pathogenic or other microorganisms, both inducing microorganisms and challenge pathogens occur on or within the protected tissue. The most common examples of cross-protection involving fungi are those which are used against vascular wilts. Inoculation with nonpathogenic or attenuated strains of pathogenic formae speciales of *Fusarium* and *Verticillium* species or with other fungi or bacteria, all have shown altered levels of cross-protection.

6. Hypovirulence

It is defined as reduced virulence of pathogen strain due to the presence of transmissible double stranded RNA. Hypovirulence was first shown to be associated with the chestnut blight fungus (*Cryphonectria parasitica*) where a different colored fungus was recovered from "healing cankers" instead of the typical orange colored *C. parasitica* fungus, a white-colored fungus was found. The chestnut blight fungus has become hypovirulent in some areas by acquiring double stranded RNA that debilitates the pathogen, thereby reducing its virulence to its host. Other examples of hypovirulence have also been reported in many other pathogens, including *Rhizoctonia solani*, *Gaeumannomyces graminis* var. *tritici* and *Ophiostoma ulmi*.

**Fungal compounds involved in induction of plant responses**

*Trichoderma* spp. released many compounds into the zone of interaction and induces resistance in plants. Fungal proteins such as xylanase, cellulase, and swollenin are secreted by *Trichoderma* species. *Trichoderma* secreted endochitinase can also enhance defense, possibly through the induction of plant defense related proteins. An additional class of elicitors of plant defense includes oligosaccharides and low-molecular weight compounds. These are released from fungal or plant cell walls by the activity of *Trichoderma* enzymes.
Systemic induction of defense-related genes and proteins
After treatment with *T. harzianum*, many defense/stress-related proteins functions were upregulated. Stress response enzymes such as oxalate oxidase and superoxide dismutase were upregulated in roots while, methionine synthases is highly upregulated in shoots. Other proteins were also upregulated in shoots which includes glutathione-S-transferase and glutathione-dependent formaldehyde dehydrogenase (FALDH), which operate as detoxifying enzymes; peroxidase, a scavenging enzyme controlling the amount of damage resulting from the oxidative burst; heat shock proteins, which are also well-known as stress proteins; oxalate oxidase, which was involved in stress and defense responses and is possibly involved in producing the oxidative burst of hydrogen peroxide; and others.

Alleviation of damage by reactive oxygen species
Reactive oxygen species (ROS) are chemically-reactive molecules containing oxygen, which includes free radicals such as superoxide anion, hydroxyl radical as well as non-radical molecules like hydrogen peroxide (H₂O₂), singlet oxygen (O₂), and so on. Under severe environmental stress, ROS production can surpass the scavenging capacity and accumulate to levels that can damage cell components, e.g., via lipid peroxidation. Roots and leaves of *Piriformospora indica* inoculated plants showed increased levels of antioxidant compounds and antioxidative enzymes and reduced levels of hydrogen peroxide.

Effect on root development and performance
Plant roots inoculated with *Trichoderma* are deeper and more robust. Main and secondary roots of maize increased in size with *Trichoderma*-T22 inoculation. Promotion of root growth and increased length of root hairs were detectable even before notable root colonization. Root branching can progress soil exploitation and therefore result in the promotion of plant growth. *Trichoderma* spp. has the potential to colonize seeds and bestow benefits to seeds and seedlings even before radicle protrusion occurs. This permits *Trichoderma* spp. to be widely used as seed treatments, which is a very cost-effective method of application.

Enhanced nitrogen use efficiency
Globally, the nitrogen (N) problem is a big one. The interaction of BCF with plants may increase the nitrogen use efficiency (NUE) in plants. This effect was first reported with *T. harzianum* T22 in maize field trials in the late 1990s. Plants grown under low soil nitrogen conditions from seeds treated with T22 were larger and darker green. Generally, plants respond to increasing nitrogen fertilizer levels with increased yield and growth up to a point when increasing nitrogen fertilizer, no longer increases yields. With the help of T22, this yield plateau was accomplished with 40–50% less nitrogen fertilizer than in its absence.

Increased nutrient uptake
*Trichoderma* spp. has considerable abilities to solubilize a range of plant nutrients that may be present in insoluble, and unavailable, forms in soils. These consist of phosphorus and minerals, including iron, copper, zinc and manganese. Additionally, even when these nutrients are completely soluble and available to plants, the presence of *T. asperellum* on cucumber roots...
grown hydroponically improved uptake of various plant nutrients. Consequently, these root symbionts possibly able both to solubilise insoluble plant nutrients and also to induce plants to absorb more of soluble nutrients, which implies at least two mechanisms occurs through which availability to the plant may be improved.

**Increased photosynthetic rate**

Plants colonized by *Trichoderma* are not only larger, but also greener. High photosynthetic rates coupled with low transpiration rates indicate high water use efficiency. The action of *Trichoderma* spp. that contributes to the improvement of root growth and distribution was also considered as a key feature to the prolonged photosynthetic activity and the delayed senescence in rice plants. Additionally, *Trichoderma* spp. was recently reported as having the potential to degrade cellulose. Cellulose degradation may release a bulk amount of Nitrogen in the rhizosphere of rice plant. High N concentration uptake has positive correlation with photosynthetic rate.

**Conclusion**

Biocontrol fungi (BCF) reduce the harmful effects of plant pathogens and encourage positive responses in the plant through different mechanisms. *Trichoderma* species induce growth in addition to ISR. The abilities of BC fungi to induce resistance to biotic stresses such as disease and increases NUE, photosynthetic rate and increased nutrient uptake make them extremely useful tools with which to increase plant productivity, improve food security, and improve the environment.

**References**


Harman GE, Petzoldt R, Comis A and Chen J. 2004. Interactions between *Trichoderma harzianum* strain T22 and maize inbred line Mo17 and effects of this interaction on diseases caused by *Pythium ultimum* and *Colletotrichum graminicola*. *Phytopathology.* 94: 147–53.
