

Evaluating potential side effects of *Trichoderma* as biocontrol agent: A two-edged sword?

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In the current need of optimizing agricultural production, endophytic fungi are increasingly seen as part of the solution. *Trichoderma*, subject of this review, colonizes the most external layers of the root, improving plant growth. This colonization also induces plant defenses, helping the plant to minimize pest damage. However, if the fungi enter vascular tissues, necrosis and nutrient competition occurs. Easily dispersed in the environment, the fungi may affect other targets, such as insects, if the spores manage to penetrate the insect cuticle. Mostly seen as a race for resources, space, and with a possible interplay of toxins, *Trichoderma* may act as a powerful bioinsecticide. Unforeseen effects on other organisms of the ecosystem and trophic chain that might get exposed are also reviewed.

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Trichoderma: a fungus with multiple applications

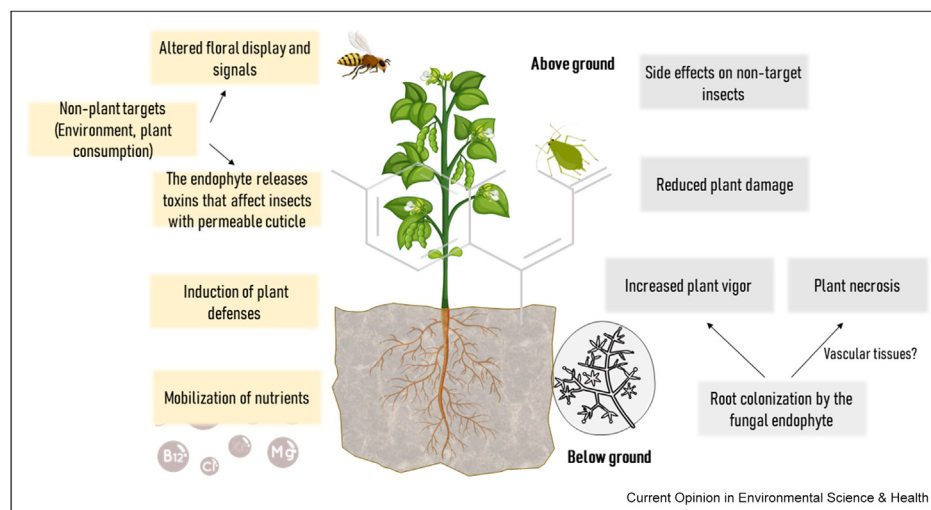
Trichoderma is a genus of filamentous fungi belonging to the family Hypocreaceae, globally distributed in many ecosystems. Generally present in soil, it mainly acts as a saprophyte, as a parasite of fungi, nematodes, and

insects, or as a plant symbiont, and can be found as a free-living organism or associated with plant roots [1]. Due to the application of current molecular taxonomic tools, it is estimated that each year about 50 new species of *Trichoderma* are recognized, having been described 460 different species until the year 2022 [2].

Different species within the genus *Trichoderma* have been widely studied and used as biological control agents (BCAs) in agriculture, due to different mechanisms of action. *Trichoderma* parasitize phytopathogenic fungi and eggs/juveniles of plant parasitic nematodes produce potent biocidal compounds (antibacterial, antifungal, oomycetocidal, nematocidal, and insecticidal), compete for space and nutrients in the rhizosphere in a very effective way, hindering its access to soil pathogens, and induces in its host plants a local and/or systemic defensive response against a possible future pathogen or pest attack [3]. In addition, different *Trichoderma* species act as plant growth-promoting fungi, or biofertilizers, through the synthesis and release of plant hormones (auxins, cytokinins, etc), the solubilization of nutrients present in the soil (such as phosphorus and potassium), or the production of siderophores to metal chelation (such as iron, copper, zinc, or magnesium). Finally, in their interaction with the plant, several *Trichoderma* species are able to induce greater tolerance under abiotic stresses, such as drought, salinity, or extreme temperatures [3]. All these mechanisms of action have led commercial *Trichoderma* formulations currently to represent 50%–60% of the biofungicides on the world market [4].

Despite all the benefits of the use of *Trichoderma* in agriculture, it can have significant adverse effects on nontarget organisms, such as plants or beneficial insects (developed in sections “*Trichoderma* as a plant pathogen” and “*Trichoderma* as entomopathogen of non-target insects” of this work). The aims of this paper are i) to collect, collate, and discuss the side effects that *Trichoderma* can have on these organisms, and ii) to try to discern why they happen and what effects they have. The infographic in [Figure 1](#) summarizes the content of these adverse effects with their possible causes and consequences.

Figure 1



Overall effects of *Trichoderma* on plant hosts, and insects feeding on plant tissues. Direct mechanisms, in yellow boxes, are mediated by nutrient mobilization, nutrient competition or the release of bioactive compounds produced by fungal endophytes, which possess the potential to directly inhibit the growth of other organisms, including insect pests. Indirect mechanisms are caused by the association between the fungi with plants, comprising changes in growth, morphology, biochemistry, and development of the host plant. Silver boxes summarize the potential side effects of *Trichoderma* inoculation that were evaluated in this review.

Plant-*Trichoderma* interaction

For effective colonization of roots by *Trichoderma* to occur, mutual recognition through molecular dialogue is necessary [5]. *Trichoderma* produces molecules recognized by root cell receptors, such as cysteine-rich hydrophobins [6], while the plant releases molecules in its exudates (carbohydrates, lipids, terpenoids, and amino acids) that are recognized by *Trichoderma*, directing its growth [7].

Once the *Trichoderma* hyphae come into contact with roots, the penetration process begins. In order to enter the root, *Trichoderma* must be able to form channels for its hyphae across the plant cell walls. Among the different proteolytic, cellulolytic, xylanolytic, and pectinolytic cell wall-degrading enzymes that are involved, we highlight the relevant role of cellulolytic enzymes, such as swollenins and ceratoplatanins [5].

Once inside the root, *Trichoderma* colonizes the cell apoplast in a parallel pattern as the defined for the root tissue. However, this colonization is limited only to the epidermis and outer cortex layers (in addition to the root surface), without reaching the inner cortex layers, or the vascular bundles [8]. Throughout the *Trichoderma*-plant symbiosis, a molecular dialogue is established in which plant cell receptors recognize microbe-associated molecular patterns (MAMPs) of *Trichoderma* (sterols, chitin, and β -glucans) in the apoplast, inducing local and systemic signals in the host plant [9].

Trichoderma as a plant pathogen

Although *Trichoderma* includes species widely used as beneficial agricultural bioinoculants, different cases of pathogenic behavior by these species on different crops have been reported over the years. *Trichoderma* is mainly a fungus present in the soil, interacting with the rhizosphere; therefore, a possible pathogenic behavior may appear in the roots. In Jiangxi province, China, the death of about six thousand *Polygonatum cyrtoneuma* plants was reported in 2022 as a consequence of root infection by *Trichoderma virens*, causing sunken red-brown lesions, also on tubers [10*]. This pathogenic behavior on roots that serve as the plant's reserve store had already been observed recently for *Trichoderma asperellum*, the causal agent of green mold disease on sweet potato [11]. With the evidence reported so far, there may be a pathogenic behavior of *Trichoderma* on reserve roots, tubers, or bulbs, since they represent an important source of nutrients for a fungus that also behaves as a saprophyte. Therefore, it is necessary to investigate why this behavior occurs and whether it can affect other crops of great economic importance within this group, such as potato, beet, or onion, which would imply testing commercial products with these crops before their massive use. This reported pathogenic behavior of *Trichoderma* could be of secondary type, after the attack of another pathogen of these crops, which requires further studies in this respect.

In addition, *Trichoderma* can infect the root systems of other plants. The ability of *Trichoderma longibrachiatum* to infect the roots of red leaf lettuce [12*], causing its

death, has been described, as well as of *Trichoderma viride* on tomato, bell pepper, cucumber [13], and pine tree [14]. The reason why *Trichoderma* eventually kills its host has been associated with various causes, such as surface colonization of the root, which causes the plant to be unable to absorb nutrients and/or water [12], or direct maceration of root tissues [13]. Moreover, *Trichoderma* can penetrate through the roots of its host plant and cause lesions in the aerial part of the plant, as is the case of *Trichoderma koningii* in maize plants, causing internodal lesions and extensive necrosis on roots [15,16].

However, *Trichoderma* does not require root penetration to behave as a pathogen, having been described as a causal agent of diseases directly on leaves and post-harvest products. In leaves of *Curcuma wenyujin* and *Dendrobium nobile*, the fungi *Trichoderma koningiopsis* and *T. longibrachiatum*, respectively, were identified as the causal agents of yellowing, wilting, and black circular spots confirmed by Koch's postulate [17,18]. In the case of postharvest produce, different *Trichoderma* species have been described to colonize tissues and produce important diseases. In maize ears, *Trichoderma afroharzianum* has been found as the causal agent of a new disease (ear rot), confirmed by its isolation from crop fields in Southern Germany and its re-inoculation by silk channel ears under controlled conditions [19]. This pathogenic behavior has also been reported on citrus fruits, e.g. from the previously described *T. viride* causal agent of pine dieback on lemon fruits [14]. Similarly, in 2009, *Trichoderma atroviride* was described for the first time as a causal agent of mandarin fruit rot, after harvest, degreening, and storage under ambient conditions [20]. The mechanisms involved in the behavior of *Trichoderma* as a pathogen of aerial plant organs are so far unknown. Therefore, in order to avoid and/or prevent eventual damages when used as plant growth-promoting fungi or BCAs, it becomes crucial to get understanding on the reasons behind the pathogenic behavior of *Trichoderma*, and what are the mechanisms involved.

How and why *Trichoderma* behaves as a plant pathogen?

How a beneficial symbiont organism becomes a pathogen under certain conditions and with certain hosts is one of the questions to be deciphered in the coming years. Several studies have been carried out on this subject, under different perspectives. Some of them have analyzed and compared the genomes of different species of *Trichoderma*, reaching the conclusion that mycoparasitism must have been the ancestral life form of these fungi. Subsequently, the presence of phytopathogenic fungi and root exudates in the rhizosphere (both *Trichoderma* food sources) led to an evolutionary change of *Trichoderma* into a plant symbiont fungus after successfully colonizing the plant root [21,22].

More recently, a novel work has gone a step forward in the explanation of the evolution of *Trichoderma* from mycoparasite to beneficial fungus [23*]. From an evolutionary perspective, several *Trichoderma* species were brought into contact with model plants *Marchantia polymorpha* (liverwort), *Dryopteris affinis* (pteridophyte), and *Arabidopsis thaliana* (angiosperm). None of the *Trichoderma* species used showed pathogenic behavior on the pteridophyte and angiosperm. However, *T. virens*, *T. brevicompactum* and *T. hamatum* behaved as pathogens on liverworts, colonizing their tissues and sporulating on them. Furthermore, it was reported how the exogenous addition of salicylic acid (SA) in these liverworts prevented the pathogenic behavior of *Trichoderma* [23*]. Therefore, *Trichoderma* could have had an evolutionary moment in which it behaved as a plant pathogen. The development of the SA-mediated defensive response by plants would have been the key that favored a symbiotic behavior of the fungus.

In addition to phytopathogens, beneficial microorganisms also have to be able to override or bypass the defenses of their host plant in order to colonize it [24]. In the case of SA, several beneficial microorganisms require suppression of their signal on roots in order to colonize them effectively, such as nodule-forming rhizobacteria [25], endophytic fungi [26], and even arbuscular mycorrhizal fungi (AMF) [27]. Moreover, it has been described a pathogenic behavior on the liverwort *M. polymorpha* in the particular case of AMF. Similarly to *Trichoderma*, such pathogenic behavior is mediated by the absence of a plant defensive response mediated by SA [28].

The role of SA in the success of root colonization by *Trichoderma* has been addressed in recent years [29]. In the first hours of *Trichoderma*-root interaction, there is a decrease in the expression of SA-related genes locally, leading to a momentary suppression of the plant's defensive responses, which is quickly recovered [30,31]. Several works have used SA-deficient ethylene signaling mutants of *A. thaliana* to elucidate the behavior of *Trichoderma*. With *Trichoderma harzianum*, the absence of a locally SA-mediated defensive response in the roots of the *sid2* mutant led to massive root colonization by the fungus, reaching the vascular bundles. In this case, *Trichoderma* behaved as a pathogen, rotting all plant tissues, from roots to leaves [32]. Similarly, root colonization of the tomato *sid2* mutant by *T. harzianum* was greater than in the wild ecotype [33]. Therefore, SA plays a key role in the behavior of *Trichoderma* as a plant symbiont, since in its absence it becomes a systemic pathogen.

Although, so far, the explanations for why *Trichoderma* behaves as a pathogen are linked to the ability of the host plant to defend itself, there could be other explanations not yet addressed. For example, the symbiosis

may appear after *Trichoderma* mutations that may modify its way of recognizing the plant as a symbiont. It is also noteworthy that there are many fungal genera that include both pathogenic and endophytic species (and even strains) for the same host plant. This could be the case of *Trichoderma*, having to start considering the genus as a mixture of beneficial and pathogenic fungi. In addition, current climatic changes could induce in *Trichoderma* and in its host plants important changes, such as a weakening of plant defenses or a greater aggressiveness of *Trichoderma* in its behavior as a saprophyte, leading to an attack on healthy plant tissues. These physiological changes in plant and fungus would be a direct consequence of extreme situations derived from climate change, such as drought, which weakens plant defenses and can induce pathogenic behavior in the fungus, necessary for its survival in niches without other sources of nutrients.

Development of *Trichoderma* bioinsecticides

Bioinsecticides are insect-pest control agents based on living microorganisms or the natural products they produce. Similar to the use of *Trichoderma* strains as biofungicides, the inhibition of insect growth is produced either by direct inhibition mechanisms, such as nutrient scavenging or producing fungal secondary metabolites that compromise insect growth, or the activation of plant defense mechanisms that would deter the insect that feeds on the plant material [34]. Even though the insecticidal potential of the genus *Beauveria* has been reported to be the most important [35,36], *Trichoderma* is proven to act as a contact bioinsecticide against some hemipteran pests, such as aphids with soft cuticula, or mirid bugs [37*]. Although the mode of action is yet to be fully understood, plant sap analyses and feeding behavior seem to indicate that bug deterrence is unlikely to be explained by changes in sap nutrient composition, thus pointing out at direct inhibition mechanisms according to the division stated here above.

Direct insect deterrence would i) imply that the fungal conidia have entered the insect via the chitinous cuticle. The use of a surfactant is often necessary to assure contact between fungal spores and the cuticle. Once the spores have entered the insect body, ii) they differentiate into blastospores. The insect's lifespan is then shortened due to production of insecticidal toxins, which are species-dependent. Toxins might impair the insect metabolism. Moreover, the fungal subsequent phases of growth rely on iii) the development of fungal mycelia, which will consume the host nutrients in the haemolymph [38–40]. The fitness of insect pests, such as aphids or whiteflies, is especially affected by the availability of nitrogen sources, such as amino acids, which will be readily consumed by 178 of the fungi [41,42].

The most challenging part of bioinsecticide strategies with *Trichoderma* is optimizing the spray strategy, since pipetting fungal spores, such as performed in many lab trials is not representative of using bioinsecticides in agricultural setups, either in greenhouses or open fields. However, since promising results have been noticed, more research is necessary in using the most effective fungal concentration and spray strategy [43].

Trichoderma as entomopathogen of nontarget insects

A growing number of studies have reported possible cascading effects when using in crop production and plant protection endophytic fungi, such as *Trichoderma*, as they may affect arthropods with which the plant interacts [44]. However, most of these studies have focused on the three-way interaction between beneficial fungi and pest arthropods via the induction of plant defenses [44]. One of the interactions that could get affected by the fungal endophyte is that between plants and their pollinators. Such interaction might get unbalanced by the fungal-boosted plant vigor, which may in turn affect blooming period and production of flowers [45]. This indirect effect would not imply pathogenicity but may affect the fitness of the insect via nutrient availability and foraging costs. On the other hand, secondary metabolites are one of the most studied effects of fungal inoculation in the roots [46], but we know have direct proof that plant sap metabolites finally arrive at the floral tissues [47]. Once there, secondary metabolites impaired by the fungus may affect floral attractiveness to pollinators via the fraction of plant secondary compounds that are volatile and contribute to floral scent. In this regard, it becomes necessary to bring together the effects of natural enemies and plant pathogens on volatile organic compounds (VOCs) into plant pollination studies.

In line with recent investigations in microbial ecology, the inoculation with a fungus such as *Trichoderma*, that may establish in the insect's internal tissues, is also subjected to cascade effects. In that sense, the microbe that arrives first would decrease the chances of subsequent microbes to colonize, a mechanism that is overall known as "priority effects" [48]. In the particular case of nonharmful insects, it is known that they have a community of gut microbiota composed by yeasts and bacteria, being core and noncore. This microbiota is first acquired via the parental line during insect development. This vertical transmission often leads to consistent microbial features across populations, known as "core microbiota." This core microbiota is later enriched via environmental inputs, mainly via feeding resources [49]. Inoculation with *Trichoderma* might affect the dynamic of gut colonization, thus finally affecting insect individual lifespan, and ultimately, even colony fitness [50].

Microorganisms in the endosphere also promote plant defense against herbivores both above and belowground by providing feeding deterrence or antibiosis. One direct consequence on herbivores would be the induction of associated molecular patterns in plants, but, furthermore, fungi that get to inhabit floral nectar and insect honeydew may produce VOCs that attract beneficial insects like natural enemies of the herbivore. Doing so, they provide indirect pest control in a four-way ecological interaction involving plants, fungi, the insect pest, and its natural insect enemy [43].

Conclusions and proposals for future studies

About 60% of all fungal-based BCAs are contributed by *Trichoderma*-based biopesticides, which are available in different formulations. It is the most popular due to its diverse mechanisms of biocontrol that include antibiosis, colonization, competition, direct mycoparasitism, etc. This makes these fungi a powerful tool to be used in many crops and agricultural setups, but, on the other hand, also makes effects on nontarget organisms more feasible.

The pathogenicity of *Trichoderma* for plant hosts is mediated by a complex signal interplay between the plant and the fungi at the root cortex. It is impossible to gather the whole complexity of external signals that may modulate a molecular response, but current biochemical and molecular annotation and expression tools definitely help to understand the mechanism base and thus gather predictive responses in new applications, such as new plant crops or even cultivars within the same crop [37]. More strikingly, *Trichoderma* may act as pathogen in aerial plant organs, such as leaves, where mechanisms involved are yet not understood. Gathering such knowledge is, of course, key to prevent the transition from symbiont to pathogen that is specifically reviewed in this piece.

This review has pointed out that direct and indirect interactions between beneficial partners, for instance, exemplified by pollinating arthropods and endophytic fungi, can strongly modify the final impacts on crop yield and, therefore, deserve specific attention by the research community. There is potential to use synergistic actions between plant mutualistic counterparts to increase yield, but, more importantly, moving away from the traditional separation among fields (entomology and microbiology) would positively impact our power to predict yields in more realistic crop scenarios, where all players act at once. Given the multiple benefits of microorganisms to plants and the existence of cascade effects with insects on different trophic levels, we argue that future pest management strategies should consider and exploit the whole range of possibilities that microorganisms offer to enhance plant defense and increase attraction, fecundity, and performance of natural

enemies. The exploration of such interplay is particularly favored by the current framework of further limiting chemical pesticides.

Even though testing potential side effects on arthropods is already a great scientific challenge, due to the need of testing different conditions, crops, or even varieties, there are noninsect plant pests that could be also affected by *Trichoderma* inoculation, such as nematodes [51]. On a wider ecological context, it is important to note that there is growing concern about the potential of *Trichoderma* species of being causal agents of human mycoses, which has been largely disregarded [52*].

Authorship contribution statement

JP conceptualized and designed the manuscript. JP and MIP drafted the first version of the manuscript and performed all revisions. BH, JMG, and OS contributed to proofreading and critical reading of the manuscript. All authors have read and accepted the published version of the manuscript.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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This study describes a possible role of the widely distributed *Trichoderma* against human health, which has been neglected so far.