frontiers | Frontiers in Agronomy

TYPE Opinion
PUBLISHED 28 March 2024
DOI 10.3389/fagro.2024.1386568

Check for updates

OPEN ACCESS

EDITED BY
David Ezra,
Agricultural Research Organization (ARO), Israel

REVIEWED BY
Jorge Poveda,
University of Valladolid, Spain

*CORRESPONDENCE
Mª Isabel Trillas
mtrillas@ub.edu

RECEIVED 15 February 2024
ACCEPTED 13 March 2024
PUBLISHED 28 March 2024

CITATION
Trillas MI, Segarra G and Avilés M (2024) Is *Trichoderma* ear rot on maize really a new dangerous plant disease? *Front. Agron.* 6:1386568. doi: 10.3389/fagro.2024.1386568

Is *Trichoderma* ear rot on maize really a new dangerous plant disease?

Mª Isabel Trillas[1]*, Guillem Segarra[2] and Manuel Avilés[3]

[1]Plant Physiology Department at Faculty of Biology, University of Barcelona, Barcelona, Spain, [2]Serra Húnter Fellow, Plant Physiology Department at Faculty of Biology, University of Barcelona, Barcelona, Spain, [3]Agronomy Department at School of Agronomy Engineering (ETSIA), University of Sevilla, Sevilla, Spain

KEYWORDS

corn ear rot disease, *Trichoderma*, Europe, mycotoxins, *Fusarium*

Introduction

Trichoderma ear rot disease in maize was first described in 1973 (Shurtleff et al., 1973). The *Compendium of Corn Diseases* considers several fungi as "secondary invaders", including *Trichoderma* spp., which often cause disease after severe leaf damage induced by other fungi or ear damage from *Helminthosporium maydis* infection. Disease caused by *Trichoderma viride* is listed as "other corn ear rots" and is associated with injury to the developing ear (White, 1999). Several publications associate *Trichoderma* spp. infections with other leaf or ear diseases, being related to damage (by weather conditions or insects) to the developing ear that provides access to windblown spores and rainfall (Vincelli, 2014; Wise et al., 2016; OSU, 2020). In short, diseases caused by *Trichoderma* spp. are sporadic, scattered within a field, and only occur when there is previous damage to the plant (from insect feeding and heavy storms). However, it has recently been reported that very aggressive strains of *Trichoderma afroharzianum* are the primary agent producing ear rot disease in the warmer regions of southern Germany and France (Pfordt et al., 2020b) as well as Italy (Sanna et al., 2022).

According to Wise et al. (2016), ear rot fungi associated with mycotoxins include *Aspergillus flavus*, *Fusarium verticillioides* (primary fungus causing *Fusarium* ear rot), as well as *Gibberella zeae* (syn. *Fusarium graminearum*), *Diplodia maydis* (syn. *Stenocarpella maydis*), and *Diplodia macrospora* (syn. *Stenocarpella macrospora*) in specific regions but not in others, suggesting a significant reliance on environmental factors. Therefore, *Penicillium* is capable of producing mycotoxins only under conditions of high humidity, and regarding *Trichoderma*, it appears that only certain species have been observed to produce mycotoxins on previously damaged maize kernels.

Before the widespread use of molecular techniques, it was difficult to identify the isolates of *Trichoderma* spp. based solely on morphological traits. Thus, the scientific literature is full of misleading identifications of *Trichoderma*. Druzhinina et al. (2005) set up the basis for correct *Trichoderma* identification through the use of advanced molecular tools. *Trichoderma* spp. are among the most common filamentous fungi isolated from soil, rotting wood, other fungi, and innumerable substrates (Druzhinina et al., 2011; Kubicek et al., 2011). Moreover, *Trichoderma* rhizosphere-competent strains interact with plants, increasing mineral uptake and activating the plant immune system with the subsequent increase of plant growth and resistance to a range of pathogens and abiotic stress (Yedidia et al., 1999; Gupta and Bar, 2020). Both induced systemic resistance (ISR) and systemic acquired resistance (SAR) have been described in *Trichoderma*–plant root interactions; the signaling molecules include salicylic acid (SA), jasmonic acid, and ethylene (Pieterse et al., 2014; Kubicek et al., 2019). The physical interaction of *Trichoderma*–plants is limited to the root epidermis, primary cell layers, and outer cortex, requiring a temporary suppression of SA-dependent plant defenses (Yedidia et al., 1999; Alonso-Ramírez et al., 2014; Poveda et al., 2020). A recent study on the coevolution of the interactions of plant–*Trichoderma* spp. using liverwort, pteridophyte, and angiosperm models suggested that the fungus behaved as a pathogen until plants developed the defense system based on SA, thus limiting its colonization (Poveda et al., 2023).

Samuels and Hebbar (2015) recorded *Trichoderma* populations ranging from 10^2 to 10^3 spores/g of soil or root, while Wolna-Maruwka et al. (2017a) found natural populations of *Trichoderma harzianum* and *Trichoderma atroviride* occurring at 3.4×10^2 spores/g of dry soil in field experiments in Poland. In another study, Wolna-Maruwka et al. (2017b), again only counting *T. harzianum* and *T. atroviride*, found 0.36×10^2 spores/g of dry soil in the control samples from their field experiment. Oskiera et al. (2017), using a newly developed multiplex PCR technique, identified 10^3–10^4 CFU/g of naturally occurring *Trichoderma* spp. in Polish soil collected from a field experiment.

The biodiversity of the genus *Trichoderma* (teleomorph *Hypocrea*, Ascomycota) has been studied in several publications. Interestingly, Jaklitsch and Voglmayr (2015) classified 650 species of *Trichoderma* from different European climate regions using *tef1* sequence data. The *tef1* gene is considered the most useful reference gene to identify and distinguish the different *Trichoderma* species (Samuels and Hebbar, 2015). In the publication discussion of Pfordt et al. (2020b), some concerns were raised about the potential production of mycotoxins by aggressive strains of *T. afroharzianum*. However, Degenkolb et al. (2008) considered the Brevicompactum clade a separate lineage in *Trichoderma*/*Hypocrea* that contains *Trichoderma brevicompactum* and the new species *Trichoderma arundinaceum*, *Trichoderma turrialbense*, *Trichoderma protrudens*, and *Hypocrea rodmanii*. With the exception of *H. rodmanii*, all members of this clade produce trichothecene-type toxins. Degenkolb et al. (2008) also re-identified the trichothecene-producing *T. harzianum*, *T. viride*, and *Hypocrea* sp. as *T. arundinaceum*. In several publications, including Kubicek et al. (2019), *Trichoderma reesei* has been recently recognized as the model organism for the industrial production of cellulolytic enzymes. Other *Trichoderma* spp. are opportunistic species in mushroom farms (*Trichoderma aggressivum*) or can become pathogens in immunocompromised people (*Trichoderma longibrachiatum*) (Komon-Zelazowska et al., 2007; Druzhinina et al., 2008). Degenkolb et al. (2008) stated that the species in the Brevicompactum clade are not closely related to the *Trichoderma* species that have biological applications in agriculture.

In Europe, for a microorganism strain (active substance) to be registered as a microbial plant protection product (PPP), it should demonstrate that it is safe for humans and the environment. According to the EU Regulation 1107/2009, several studies should be performed to prove that the PPP does not produce/contain any toxic metabolite of human concern. Risk assessment is also required to indicate the background levels of the product in the environment (air, water, and soil) after field/greenhouse application at the recommended doses and use pattern in the crop and after harvest. To be able to authorize a product as PPP for use in certain crops/diseases, Good Experimental Practice (GEP) studies are required [according to the standards of the European and Mediterranean Plant Protection Organization (EPPO)] to prove the product's efficacy and the absence of phytotoxicity to the plants on which it is being applied. Furthermore, other observed benefits may be claimed, such as yield increases and reductions in mycotoxin contents, for example, if such effects are observed during the GEP efficacy trials. Three doses as well as the mode of application (on seeds, soil/substrate, drip/air irrigation, etc.) of the authorized PPP are required by the authorities to grant authorization to a product. The dossier on the proposed PPP is assessed and reviewed by member states and the European Food Safety Authority (EFSA) before being finally approved or not by the EU Commission (Trillas et al., 2020).

The disease triangle

Environmental and agronomic practices and field site

As described in all plant pathology books, the disease triangle is important to assess disease. In addition to the pathogen and the plant host, the environment (temperature, relative humidity, and precipitation) are key factors in the plant disease triangle. Such information was not reported in detail in the work from Pfordt et al. (2020b) to assess the environmental conditions and the management practices of the crop from where the *Trichoderma* isolates were obtained. The publication briefly cited the growing conditions of the maize: "symptoms observed in Southern Bavaria, after warm and dry summer". However, this information and the agronomic practices were already known because research on complex *Fusarium* ear rot was conducted from 2016 to 2018 in 58 locations in Germany, including the same fields from where the isolates of the *Trichoderma* spp. were obtained (Pfordt et al., 2020a). In these fields, Pfordt et al. (2020b) recorded the mean temperature and precipitation in July (during flowering when the impact of *Fusarium* disease was the highest) but did not report on the climatic condition during the growing season and the insect pest management strategy used. Furthermore, information on the temperature (23°C) under seasonal day/night light cycles was given for the greenhouse experiments assessing the pathogenicity of the *Trichoderma* strains, but all the other environmental conditions were not mentioned.

Co-occurrence of *Trichoderma* and *Fusarium*

Pfordt et al. (2020b) mentioned that "surprisingly" in 2018, a "severe occurrence" of *Trichoderma* on maize was recorded at "a field site" in Southern Germany, but its specific location was not provided. This field has been also used to study a *Fusarium* species complex, using artificial inoculation of the pathogen, which is detailed in the supplementary materials of Pfordt et al. (2020a, 2020c). The level of disease indicated by "severe occurrence" could have been specified more accurately as the number of cobs with *Trichoderma* ear rot compared to the uninfected controls or in relation to other *Fusarium* ear rot diseases or maize plants with *Fusarium* disease. *Fusarium* diseases are not mentioned at all in Pfordt et al. (2020b), where the *Trichoderma* spp. may be associated with *Fusarium* spp. mycoparasitism. There is evidence that endophytic *Fusarium* species cause symptomless infections in kernels (Gromadzka et al., 2019), with the incidence of symptomless *Fusarium* infections being higher than that of kernel rot. The finding that *Fusarium* can be endophytic is well documented in several publications, which report that the fungus is found in the embryo and endosperm of kernels and is associated with animal toxicity (Bacon et al., 1992; Yates et al., 1997). The presence of *Fusarium subglutinans* and *F. verticillioides* together with *T. atroviride* was previously reported in maize ears with significant *Fusarium* ear rot in Poland from 2014 to 2017 (Gromadzka et al., 2019). In fact, studies performed in Poland (Gromadzka et al., 2016) indicate the co-occurrence of *Fusarium* spp. with other fungi in the same kernel, with *T. atroviride* being the most abundant species (31%). Consequently, our opinion is that in opposition to what is claimed by Pfordt et al. (2020b), *Trichoderma* spp. are present in the maize ear rot not as a primary pathogen but in co-occurrence with *Fusarium* spp. as described in several studies in Poland (Gromadzka et al., 2019).

Maize plants

Pfordt et al. (2020b) should have mentioned the maize hybrids used in the greenhouse experiments (The Methodology) to test the pathogenicity of the *Trichoderma* isolates. It has only been stated that "maize seeds of two varieties" were used. Moreover, in the Introduction, there is no mention of the maize hybrids from where the *Trichoderma* spp. isolates were obtained, other than stating that the cobs of "20 maize varieties" were sampled. In Pfordt et al. (2020c), it is mentioned that four susceptible maize varieties were used for the inoculation with different *Fusarium* species to evaluate their pathogenicity and mycotoxin production. It is known that the development of maize hybrids resistant to *Fusarium* ear rot is important to minimize the risks of mycotoxin (Pascale et al., 2002). For example, the use of maize hybrids that are genetically engineered with the genes expressing the cry toxin of *Bacillus thuringiensis* is important since the incidence of symptomless *Fusarium* infections in kernels is reduced when compared with the near-isogenic hybrids (Munkvold et al., 1997).

The methodology

Greenhouse study to assess pathogenicity

In Pfordt et al. (2020b), Table 1, isolate Tri1 from France as well as isolates Tri2, Tri3, Tri4 (2018), and Tri5 (2019) from Germany were obtained from the plants with symptoms of *Trichoderma* ear rot), while the other 15 isolates tested were obtained from different sources. In Pfordt et al. (2020b), Table 2, after artifical inoculation, significant differences in disease severity (lowest disease levels) were observed for *T. harzianum* T39 (commercial microbial PPP) and *T. harzianum* T12 (university strain with potential biocontrol activity). The highest disease severity was observed for the *T. afroharzianum* Tri1, Tri2, Tri3, and Tri5 isolates. No disease was observed in the greenhouse study with Tri4 (*Trichoderma tomentosum*), which had been isolated from cobs showing symptoms of *Trichoderma* disease, or with the reference type strain *T. afroharzianum* CBS124620, which had been isolated in Peru from *Theobroma cacao* plants. The fact that no disease was produced by the reference type strain was attributed to the possible loss of pathogenicity, while no comments were made about the non-pathogenicity of *T. tomentosum*. Since silk channels have a complex and dynamic microbiome that is rich in nutrients (Khalaf et al., 2021), another possibility is that the reference type strain may prefer different carbon sources. *T. tomentosum* and *T. harzianum* remain in the Green/Harzianum clades (Jaklitsch and Voglmayr, 2015), while *T. harzianum* and *T. afroharzianum* belong to the Harzianum/Virens clades (Kubicek et al., 2019). They do not belong to the Brevicompactum clade.

The strains associated with *Trichoderma* ear rot in Europe

T. atroviride was reported to occur in 14% of the maize samples examined between 2014 and 2017 in Poland (Gromadzka et al., 2019). Earlier studies by the same research group (Blaszczyk et al., 2011; Blaszczyk et al., 2017) reported that *T. atroviride* accounted for a minor proportion of the isolates obtained from samples, with *T. harzianum* being the prevalent species in Poland. It is worth noting that Gromadzka et al. (2019) also reported that competitive species of *T. atroviride* reduced the mycotoxin content in maize samples. Other *Trichoderma* spp. also reduce mycotoxins *in vitro* and *in planta* (Modrzewska et al., 2022; Dini et al., 2022). Sanna et al. (2022) classed two strains of *T. afroharzianum* as being responsible for seed rot in maize in Italy by also using artificial inoculation experiments based on the method described by Pfordt et al. (2020b).

Artificial inoculation

The silk channel inoculation method is widely used to evaluate resistance/susceptibility to *Fusarium* ear rot (Mestarhazy et al., 2020). Other methods have not been compared and may be more appropriate, such as the needle pin and toothpick or spraypulverization technique. Pfordt et al. (2020c) tested two spore densities and two inoculation methods in the pathogenicity tests on maize cobs in field conditions, using a spore density of 10^4 spores/mL for *F. graminearum* and 10^6 spores/mL for the other *Fusarium* spp. Their findings indicated that the aggressiveness of *F. graminearum* may be higher than that of the other *Fusarium* species. In the assay used by Pfordt et al. (2020b), to assess pathogenicity, there was no justification for using such a high concentration of spores of 10^6 conidia/mL of *Trichoderma*. Such high concentrations of *Trichoderma* are extremely unlikely to occur in the air and have never been described in the literature. Moreover, saprotrophy is a very ancient trait that is widespread in the *Trichoderma* genus and fungi and could also occur in the rhizosphere and soil. Mycoparasitism is also found, but only a few species of *Trichoderma* have been isolated as endophytes (Druzhinina et al., 2011). The most plausible scenario is that local *Trichoderma* spp. associated with the saprotrophy and mycoparasitism of *Fusarium* spp. were responsible for the observations reported by the authors.

Final considerations

The lack of descriptions of both environmental conditions and agronomic practices, the omission that the fields from where the *Trichoderma* species were isolated were also used to study *Fusarium* ear rot, and the absence of any information on the maize hybrids used (resistant/susceptible to *Fusarium* spp.) in the work from Pfordt et al. (2020b) should be considered when trying to understand the importance of *Trichoderma* ear rot in Germany. Moreover, the work reported by Pfordt et al. (2020b) did not mention the well-documented fact that only specific *Trichoderma* species in the Brevicompactum clade produce mycotoxins. This is an important identity characteristic that should have been investigated.

From the results reported by Pfordt et al. (2020b), it is questionable if the appropriate methodology was used to evaluate *Trichoderma* ear rot. Furthermore, there is weak evidence for the involvement of *T. afroharzianum* that "mutate into aggressive plant pathogens" (not reported by researchers in North America). In summary, as scientists and according to the International Biocontrol Manufacturers Association (IBMA), it is very important to investigate the real importance of *Trichoderma* ear rot in Europe and also determine whether *Trichoderma* is a secondary or a main agent responsible for disease by performing studies under realistic conditions—which encompasses the method of infection and the concentrations used—and employing appropriate molecular identification tools for differentiating between putative "aggressive" strains. In the USA, the occurrence of *Trichoderma* ear rot has not hampered the use of commercial *Trichoderma* strains. Is *Trichoderma* ear rot on maize really a new dangerous plant disease or is *Trichoderma* actually part of the solution by reducing mycotoxin contents in corn?

Author contributions

MT: Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing, Data curation, Investigation, Methodology, Validation. GS: Conceptualization, Validation, Writing – original draft, Writing – review & editing, Data curation, Investigation, Methodology, Supervision. MA: Writing – review & editing, Data curation, Investigation, Methodology, Validation, Conceptualization, Supervision, Writing – original draft.

Funding

The author(s) declare that financial support was received for the research, authorship, and/or publication of this article. Publication was supported by UB-Biocontrol Technologies Chair in Microorganisms for Agriculture.

Conflict of interest

MT and MA are partners in the University of Barcelona spin-off company Biocontrol Technologies, S.L.

The remaining author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Alonso-Ramírez, A., Poveda, J., Martín, I., Hermosa, R., Monte, E., and Nicolás, C. (2014). Salicylic acid prevents Trichoderma harzianum from entering the vascular system of roots. *Mol. Plant Pathol.* 15, 823–831. doi: 10.1111/mpp.12141

Bacon, C. W., Bennett, R. M., Hinton, D. M., and Voss, K. A. (1992). Scanning electron microscopy of *Fusarium moniliforme* within asymptomatic corn kernels and kernels associated with equine leukoencephalomalacia. *Plant Dis.* 76, 144–148. doi: 10.1094/PD-76-0144

Blaszczyk, L., Basinska, A., Cwiek, H., Gromadzka, K., Popiel, D., and Stepien, L. (2017). Suppressie effect of *Trichoderma* on toxigenic *Fusarium* species. *Pol. J. Microbiol.* 1, 85–100. doi: 10.1007/s11557-008-0563-3

Blaszczyk, L., Popiel, D., Chelkowski, J., Koczyk, G., Samuels, G. J., Sobieralski, K., et al. (2011). Species diversity of *Trichoderma* in Poland. *J. Appl. Genet.* 52, 233–243. doi: 10.1007/s13353-011-0039-z

Degenkolb, T., Dieckmann, R., Nielsen, K. F., Gräfenhan, T., Theis, C., Safari,, et al. (2008). The *Trichoderma brevicompactum* clade: a separate lineage with new species, new peptaibiotics and mycotoxins. *Mycol. Prog.* 7, 177–219. doi: 10.1007/s11557-008-0563-3

Dini, I., Alborino, V., Lanzuise, S., Lombardi, N., Marra, R., Balestrieri, A., et al. (2022). *Trichoderma* enzymes for degradation of Aflotoxin B1 and Ochratoxin A. *Molecules* 27, 3959. doi: 10.3390/molecules27123959

Druzhinina, I. S., Komon-Zelazowska, M., Kredics, L., Hatvani,, L. Antal, Z., Belayneh, T., et al. (2008). Alternative reproductive strategies of *Hypocrea orientalis* and geneetically close but clonal *Trichoderma longibrachiatum*, both capable of causin invasive mycoses of humans. *Microbiology* 154, 3447–3459. doi: 10.1099/mic.0.2008/021196-0

Druzhinina, I. S., Kopchinskliy, A. G., Komon, M., Bissett, J., Szakacs, G., and Kubicek, C. P. (2005). An oligonucleotide barbacode for species identification in *Trichoderma* and *Hypocrea*. *Fungal Genet. Biol.* 42, 813–828. doi: 10.1016/j.fgb.2005.06.007

Druzhinina, I. S., Seidl-Seiboth, V., Herrera-Estrella, A., Horwitz, B. A., Kenerley, C. M., Monte, E., et al. (2011). *Trichoderma*: the genomics of opportunistic success. *Nat. Rev. Microbiol.* 9, 749–759. doi: 10.1038/nrmicro2637

Gromadzka, K., Blaszczyk, L., Chelkowski, J., and Waskiewicz, A. (2019). Occurrence of mycotoxigenic *Fusarium* species and competitive fungi on preharvest maize ear rot in Poland. *Toxins* 11, 224. doi: 10.3390/toxins11040224

Gromadzka, K., Górna, K., Chelkowski, J., and Waskiewicz, A. (2016). Mycotoxins and related Fusarium species in preharvest maize ear rot in Poland. *Plant Soil Environ.* 62, 348–354. doi: 10.17221/119/2016-PSE

Gupta, R., and Bar, M. (2020). "Plant Immunity, priming and systemic resistance as mechanisms for Trichoderma spp. biocontrol," in Trichoderma *Host Pathogen Interactions and Applications. Rhizosphere Biology*. Eds. A. K. Sharma and P. Sharma (Springer, India). doi: 10.1007/978-981-15-3321-1

Jaklitsch, W. M., and Voglmayr, H. (2015). Biodiversity of *Trichoderma* (*Hypocreaceae*) in Southen Europe and Macaronsia. *Stud. Mycol.* 80, 1–87. doi: 10.1016/j.simyco.2014.11.001

Khalaf, E. M., Shrestha, A., Rinne, J., Lynch, M. D. J., Shearer, C. R., Limay-Rios, V., et al. (2021). Transmitting silks of maize have a complex and dynamic microbiome. *Sci. Rep.* 11, 13215. doi: 10.1038/s41598-021-92648-4

Komon-Zelazowska, M., Bissett, J., Zafari, D., Hatvani, L., Manczinger, L., Woo, S., et al. (2007). Genetically closely related but phenotypically divergent *Trichoderma* species cause green mold disease in Oyster mushroom farms worldwide. *Appl. Environ. Microbiol.* 73, 7415–7426. doi: 10.1128/AEM.01059-07

Kubicek, C. P., Herrera-Estrella, A., Seidl-Seiboth, V., Martínez, D. A., Druzhinina, I. S., Thon, M., et al. (2011). Comparative genome sequence analysis underscores mycoparasitism as the ancestral life style of *Trichoderma*. *Genome Biol.* 12, R40. doi: 10.1186/gb-2011-12-4-r40

Kubicek, C. P., Steindorff, A. S., Chenthamara, K., Manganiello, G., Henrissat, B., Zhang, J., et al. (2019). Evolution and comparative genomics of the most common *Trichoderma* species. *BMC Genom.* 20, 485. doi: 10.1186/s12864-019-5680-7

Mestarhazy, A., Toth, E. T., Szwl, S., Varga, M., and Toth, B. (2020). Resistance of maize hybrids to *Fusarium graminearum*, F. culmorum, and *F. verticilloides* ear rots with toothpick and silk channel inoculation, as well as their toxin production. *Agron* 10, 1283. doi: 10.3390/agronomy10091283

Modrzewska, M., Blaszczyk, L., Stepien, L., Urbaniak, M., Waskiewicz, A., Yoshiinari, T., et al. (2022). Trichoderma versus Fusarium – inhibition of pathogen growth and mycotoxin biosynthesis. *Molecules* 27, 8146. doi: 10.3390/molecules27238146

Munkvold, G. P., Hellmich, R. L., and Showers, W. B. (1997). Reduced Fusarium ear rot and symptomless infection in kernels of maize genetically engineered for European corn borer resistance. *Phytopathol* 87, 1071–1077. doi: 10.1094/PHYTO.1997.87.10.1071

Oskiera, M., Szczech, M., Stępowska, A., Smolińska, U., and Bartoszewski, G. (2017). Monitoring of *Trichoderma* species in agricultural soil in response to application of bioprepararions. *Biol. Control* 113, 65–72. doi: 10.1016/j.biocontrol.2017.07.005

OSU (2020) *Trichoderma ear rot. Troubleshooting abnormal corn ears*. Available online at: http://u.osu.edu/mastercorn/Trichoderma-ear-rot/.

Pascale, M., Visconti, A., and Chelkowski, J. (2002). Ear rot susceptibility and mycotoxin contamination of maize hybrids inoculated with *Fusarium* species under field conditions. *Eur. J. Plant Pathol.* 108, 645–651. doi: 10.1023/A:1020622812246

Pfordt, A., Romero, L. R., Schiwek, S., Karlovsky, P., and von Tiedemann, A. (2020a). Impact of Environmental conditions and agronomic practices on the prevalence of Fusarium species associated with ear-and stalk rot in maize. *Pathogens* 9, 236. doi: 10.3390/pathogens9030236

Pfordt, A., Schiwek, S., Karlovsky, P., and von Tiedemann, A. (2020b). Trichoderma afroharzianum ear rot-a new disease on maize in Europe. *Front. Agron.* 2. doi: 10.3389/fagro.2020.547758

Pfordt, A., Schiwek, S., Rathegeb, A., Rodemann, C., Bollmann, N., Buchholz, M., et al. (2020c). Occurrence, pathogenicity, and mycotoxin production of *Fusarium temperatum* in relation to other *Fusarium* species on maize in Germany. *Pathogens* 9, 864. doi: 10.3390/pathogens9110864

Pieterse, C. M., Zamioudis, C., Berendsen, R. L., Weller, D. M., Van Wees, S. C., and Bakker, P. A. (2014). Induced systemic resistance by beneficial microbes. *Ann. Rev. Phytopathol.* 52, 347–375. doi: 10.1146/annurev-phyto-082712-102340

Poveda, J., Abril-Urías, P., Muñoz-Acero, J., and Nicolás, C. (2023). A potential role of salicylic acid in the evolutionary behaviour of *Trichoderma* as a plant pathogen: from *Marchantia polymorpha* to *Arabidopsis thaliana*. *Planta* 257, 6. doi: 10.1007/s00425-022-04036-5

Poveda, J., Eugui, D., and Abril-Urias, P. (2020). "Could *Trichoderma* be a plant pathogen? Successful root colonization in Trichoderma Host Pathogen Interactions and Applications," in *Rhizosphere Biology*. Eds. A. K. Sharma and P. Sharma (Springer, India). doi: 10.1007/978-981-15-3321-1

Samuels, G. J., and Hebbar, P. (2015). Trichoderma *identification and agricultural applications* (196, St. Paul, MN. (USA: APS Press).

Sanna, M., Pugliese, M., Guillino, M. I., and Mezzalama, M. (2022). *First report of* Trichoderma afroharzinaum *causing seed rot on maize in Italy. Disease note* (St. Paul, MN (USA: APS Press).

Shurtleff, M. C., Holdeman, Q., Horne, C. W., Kommendahl, T., Martinson, C. A., Nelson, R. R., et al. (1973). A compendium of corn diseases. *Plant Dis.* (St. Paul, MN) 76, 144–148. doi: 10.1094/PDIS.1997.81.7.723

Trillas, M. I., Casanova, E., and Segarra, G. (2020). "The development of a Biological Plant Protection Product: From Patent to Commercialisation *Trichoderma asperellum* strain T34," in *How research can stimulate the development of commercial biological control against plant diseases*. Eds. A. Cal, P. Melgarejo and N. Magan (Springer, Switzerland). doi: 10.1007/978-3-030-53238-3

Vincelli, P. (2014). *Trichoderma ear rot of corn* (Kentucky Pest News). Available at: https://kentuckypestnews.wordpress.com/2014/12/23/trichoderma-ear-rot-of-corn/ (accessed February 15, 2024).

White, D. G. (1999). *Compendium of corn diseases. 4th Edition* (St. Paul MN. (USA: APS Press).

Wise, K., Allen, T., Chilvers, M., Faske, T., Freije, A., Isakeit, T., et al. (2016). *Ear rots* (Crop protection Network). Available at: https://crop-protection-network.s3.amazonaws.com/publications/cpn-2001-ear-rots.pdf (accessed February 15, 2024).

Wolna-Maruwka, A., Kosicka-Dziechciarek, D., Piechota, T., Karwatka, K., Niewiadomska, A., Dach, J., et al. (2017a). Assessment of influence of Trichoderma sp. on the soil sanitary condition and the yield of napa cabbage. *J. Res. Appl. Agric. Eng.* 62, 197–204. doi: 10.15244/pjoes/65060

Wolna-Maruwka, A., Piechota, T., Dach, J., Szczech, M., Szczerbal, I., Niewiadomska, A., et al. (2017b). The influence of Phytosanitary status of soil and yield of red beets (*Beta vulgaris* L. subsp. *vulgaris*). *Pol. J. Environ. Stud.* 26, 847–859. doi: 10.15244/pjoes/65060

Yates, I. E., Bacon, C. W., and Hinton, D. M. (1997). Effects of endophytic infection by *Fusarium moniliforme* on corn growth and cellular morphology. *Plant Dis.* 81, 723–728. doi: 10.1094/PDIS.1997.81.7.723

Yedidia, I., Benhamou, N., and Chet, I. (1999). Induction of defense responses in cucumber plants (*Cucumis sativus* L.) by the biocontrol agent *Trichoderma harzianum*. Appl. *Environ. Microbiol.* 65, 1061–1070. doi: 10.1128/AEM.65.3.1061-1070.1999