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Inhibition of *Botritis cinerea* mycelial growth and alteration of root development of tomato seeds by soluble and volatile metabolites of *Trichoderma afroharzianum* (TR04)

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RESEARCH ARTICLE

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ABSTRACT

Botrytis cinerea is considered to be the second most important plant pathogen with devastating economic impact on different crops, including tomato. *Trichoderma afroharzianum* (TR04) is a promising biocontrol agent against fungal plant pathogens. This research evaluates its antifungal activity against *Botrytis cinerea*, its growth promoting effects on tomato seeds, and its salt tolerance. The results indicate that *T. afroharzianum* (TR04) produces both volatile and non-volatile metabolites exhibiting antifungal properties. Specifically, the culture filtrate suppressed *B. cinerea* growth by 15.99%, non-volatiles with 11.45%, and volatiles with 11.44%. In growth promotion assays, *T. afroharzianum* (TR04) metabolites did not significantly enhance tomato seed growth except for reducing primary root length compared to the control. Notably, *T. afroharzianum* (TR04) exhibited robust growth under salt stress conditions (0.5, 0.75, and 1.25M NaCl), although its morphology changed significantly, displaying yellow sporulation instead of the typical green. These results suggest *T. afroharzianum* (TR04) as a potential biocontrol agent against *B. cinerea*, even in saline environments.

KEYWORDS

secondary metabolites, antagonism, salt tolerance, biocontrol, volatile metabolites

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INTRODUCTION

Plant diseases caused by different microorganisms are responsible for extreme economic losses (Roca-Couso et al., 2021). The FAO estimates that 14% of global crop production is lost due to plant diseases, with fungi accounting for 42% and bacteria accounting for 27% (Lazarovits et al., 2014). The second most important plant-pathogenic fungus is *Botrytis cinerea* (Dean et al., 2012), which causes economic losses of USD10 to 100 billion worldwide (Roca-Couso et al., 2021). Currently, the main approach to managing *B. cinerea* relies on chemical fungicides. The primary method for controlling *Botrytis cinerea* is through chemical fungicides. However, these pesticides cause significant collateral damage to both the environment and humans (Guzmán-Guzmán et al., 2023). Therefore, developing biological control agents (BCAs) is the ideal solution to fulfill the requirements of the EU's European Green Deal - Farm to Fork strategy (European Commission, 2020).

Biological control is defined as the use of selected microorganisms that exhibit antagonistic properties to plant pathogens (Kubiak et al., 2023), such as the fungi of the genus *Trichoderma* (Guzmán-Guzmán et al., 2023). Species within the *Trichoderma* genus are successful antagonists with biocontrol properties against economically important plant-parasitic soil-borne pathogens (Yao et al., 2023).

Trichoderma exhibit antagonistic behavior against several phytopathogenic organisms through indirect or direct mechanisms such as antibiosis. Antibiosis focuses on secondary metabolites, which are volatile and non-volatile compounds (Sood et al., 2020). In addition, metabolites produced by *Trichoderma* spp. can induce profound changes in the plant phenotype such as shoot development, root branching, and cell differentiation for the formation of root hairs (Contreras-Cornejo et al., 2009; Amaresan et al., 2022).

Another problem in agriculture is salt stress, which generates ion toxicity, osmotic stress, and secondary oxidative stress, thereby damaging the physiological systems of plants (Liu et al., 2023). In recent years, the use of plant growth-promoting microbes (PGPMs) has emerged as a promising strategy to induce tolerance to salt stress in plants (Amaresan et al., 2022). The use of salt-tolerant antagonists has proven to be a valuable microbial strategy for protecting agricultural crops from fungal diseases in salty soil conditions (Kashyap et al., 2020). *Trichoderma* spp. can act by decreasing salt stress (Liu et al., 2023). Furthermore, research has demonstrated that salt-tolerant *Trichoderma* spp. possess similar potential for biological control (Liu et al., 2023).

This study focuses on *Trichoderma afroharzianum* TR04 strain and its diverse effects. Therefore, the major aims of this study were to (I) establish the presence of antagonistic volatile and non-volatile metabolites against *B. cinerea*, (II) investigate the effect on tomato seedling root development and (III) elucidate the impact of salinity stress on the growth.

MATERIAL AND METHODS

Strains and media

Trichoderma afroharzianum (TR04) was cultivated on potato dextrose agar (PDA, Biolab, Hungary) media for 5 days at 20 °C. They were previously isolated from grapevine plants (Furmint cultivar) from the Tokaj Wine Region, Northeast Hungary (Kovács et al., 2021). *Botrytis cinerea* J 5013/3 strain was isolated from green walnuts (Zabiák et al., 2025).

Agar diffusion test for pathogen inhibition by culture filtrates

Mycelial discs were collected from the freshly grown *Trichoderma* cultures and inoculated into conical flasks containing fresh 100 mL potato dextrose broth (PDB, Biolab, Hungary) and incubated at 25 °C with 150 rpm for 10 days (Marques et al., 2018). The supernatant of the cultures was collected and then filtered through a 0.22 µm Millipore filter (Yogalakshmi et al., 2021). Then, agar wells (6 mm diameter) were made in each of new PDA plates using a sterile cork borer. Mycelial plugs (6 mm) from the actively growing part of the J 5013/3 fungal pathogen (Zabiák et al., 2025) were collocated in the same day, and placed on the agar plate at a distance of 4 cm from agar well. Plates were incubated at 20 °C for 5 days. The diameter of inhibition was measured (Fig. 1A1 and B1). There were five replicates for each treatment. The effect was quantified as a percentage reduction in mycelial growth. The percentage was calculated by comparing the mean diameter of *B. cinerea* treated samples to that of the controls. The following formula was used (1)

$$I = \frac{(C - R)}{C} X\ 100 \quad (1)$$

I: Percentage of inhibition
C: Mean linear growth in control
R: Mean linear growth of pathogen in treatments

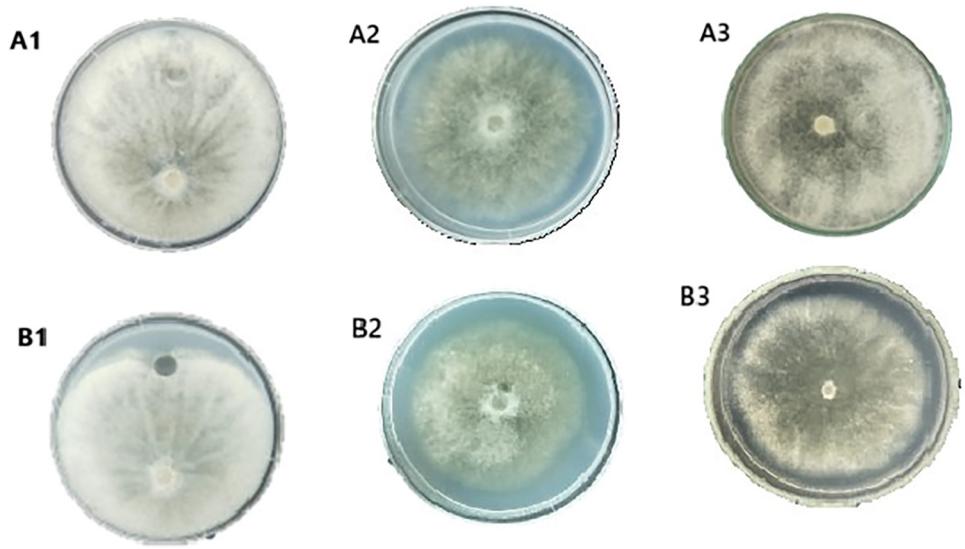

Fig. 1. Effect of secondary metabolites from *T. afroharzianum* (TR04) against *B. cinerea.* (A1) Control of culture filtrate (CFs), (A2) Control of non-volatile compounds, (A3) control of volatile compounds. (B1) Treatment of culture filtrate (CFs), (B2) Treatment of non-volatile compounds, (B3) Treatment of volatile compounds

Evaluation of the antifungal activity of *Trichoderma* non-volatile compounds against *B. cinerea*

Culture filtrates were initially prepared by transferring 5 mm mycelial discs (3 days old previously grown on PDA) (Imran et al., 2023) into conical flasks containing fresh 100 mL PDB and incubated for 10 days at 150 rpm at 25 °C (Marques et al., 2018). The resulting suspension was filtered through a 0.22 µm Millipore filter (Yogalakshmi et al., 2021). PDA medium (50 °C) supplemented with 10% (V/V) of *T. afroharzianum* (TR04) filtrates; was poured into sterile Petri dishes and inoculated with 6 mm mycelial discs of the phytopathogenic fungal strains (Yogalakshmi et al., 2021; Yassin et al., 2022). The control plates were inoculated with 6 mm mycelial discs of *B. cinerea* J 5013/3. The plates were then incubated for 5 days at 20 ± 2 °C. The diameter of inhibition was measured (Fig. 1A2 and B2). The effect was measured as a percentage compared to the mean diameter of control and inhibited mycelial growth of *B. cinerea* from the treatments, using the formula (1).

Effect of volatile compounds (VOCs) produced by *T. afroharzianum* (TR04) on the mycelial growth of *B. cinerea*

Experiments were performed by using Petri dishes (90 × 15 mm) placed in larger ones (150 × 25 mm) (Jiménez-Bremont et al., 2024). The two smaller Petri dishes contained PDA agar and were not covered with lid. One Petri dish was inoculated at the center with a 5 mm mycelial plug from an actively growing strain of TR04, while the other was inoculated with a 5 mm diameter mycelial disc of actively growing *B. cinerea*. In the control treatment, five Petri dishes contained only *T. afroharzianum* (TR04) and five Petri dishes contained only *B. cinerea*, each on potato dextrose agar (PDA), with no other microorganisms present. After inoculation, large Petri dishes were sealed with parafilm and incubated at 20 °C for 6 days, after which the growth diameters were recorded (Fig. 1A3 and B3). There were five replicates for each treatment, and the experiment was repeated twice (Meena et al., 2017). The diameter of inhibition was measured. The effect was measured as a percentage compared to the mean of the control and inhibited mycelial growth of *B. cinerea* from the treatments, using the formula (1).

Effect of *T. afroharzianum* (TR04) on tomato plant growth

The protocol for seed disinfection was developed with some modifications from Lee et al. (2016). Seeds of tomato (*Solanum lycopersicum*) were purchased commercially. Seeds were surface sterilized with 70% ethanol for 10 min, wash 3 times with distillated water. Then seeds were immersed in (20% V/V) sodium hypochlorite for 60 s with constant agitation. Finally, seeds were washed 3 times with distillated water.

The protocol was developed with some modifications from Rubio et al. (2014). An *in vitro* assay was performed to analyze the effect of *T. afroharzianum* (TR04) on tomato seedlings. On a plate of water agar (containing 2% glucose and 1% agar), we inoculated 5 mm mycelium discs. These discs were positioned directly opposite five 3-day-old germinated tomato seedlings. The plates were incubated for 14 days at ambient temperature (20–25 °C). The plates without *Trichoderma* mycelium plug were used as controls. Experiments were performed 5 times, and the plates were photographed after 14 days.

Growth of *T. afroharzianum* (TR04) under salt stress

The protocol was developed with some modifications based on Cañada-Coyote et al. (2021). Mycelial discs, 6 mm in diameter, were taken from the growing edge of the fungal colony and placed at the center of new PDA plates amended with 0.5, 0.75, and 1.25 M NaCl. Then, Petri dishes were incubated at 20 °C. Colony diameter was recorded after 3 days. The experiment was a randomized complete block with five replicates.

Statistical analysis

All *in vitro* experiments were performed in quintuplicate. Experiments were performed using a completely randomized design, and all data were analyzed using MINITAB 17 statistical software (free version). The normality of the results' distribution was determined using the Levene test (for equal variances) and the Shapiro–Wilk test (a normality test). Subsequently, data that showed a normal distribution were analyzed using a *T*-test (significance level $P < 0.05$). If, however, the data did not follow a normal distribution, a non-parametric approach was chosen, and they were compared with the Mann-Whitney *U* test.

RESULTS

In vitro mycelial growth of *B. cinerea* against *Trichoderma* through culture filtrates (CFs), non-volatiles compounds and volatile compounds

The *in vitro* application of *T. afroharzianum* (TR04) culture filtrates (CFs) demonstrated a significant ($P < 0.05$), 14.53% mycelial growth suppression of the *B. cinerea* (Table 1), resulting in a mycelial diameter of 49.4 mm, compared to the control (57.8 mm).

Regarding the antagonistic effect of non-volatile compounds, *T. afroharzianum* (TR04) showed a significant ($P < 0.05$) inhibition of *B. cinerea* mycelial growth. Nevertheless, the effect was limited. *T. afroharzianum* (TR04) caused a 10.31% reduction in growth, with a measurement of 64.40 mm, while the control sample showed 71.80 mm.

Table 1. Antagonistic effect of *T. afroharzianum* (TR04) against *B. cinerea*

Methodology	Mycelial growth (mm±SD) **Growth inhibition (%)**		*P*-value
	Treatment	Control	
Culture filtrate (CFs)*	49.4 ± 4.28[b] **14.53**	57.80 ± 1.483[a]	0.0117
Nonvolatile- compounds	64.40 ± 3.78[b] **10.31**	71.80 ± 6.02[a]	0.048
Volatile compounds (VOCs)	65.20 ± 3.19[b] **15.76**	77.4 ± 1.817[a]	0.003

*A non-parametric Mann-Whitney *U* test was employed for comparison, as the data did not follow a normal distribution.

Significant inhibition of *B. cinerea*'s mycelial growth was also observed with *T. afroharzianum* (TR04) volatile compounds ($P < 0.05$), although their effect was limited (15.76%). *Trichoderma* treated cultures exhibited a mycelial diameter of 65.20 mm, compared to 77.4 mm for the control.

Effect of *T. afroharzianum* (TR04) on tomato seedling growth

To assess the effect of *T. afroharzianum* on tomato seeds, we measured the root length, shoot length, number of lateral roots, and fresh weight of the plants. There was no significant difference in the number of lateral roots, shoot length, and fresh weight of plants (P-value > 0.05). Although, the number of lateral roots from the treatment with *T. afroharzianum* (TR04) was no significant (P-value = 0.461), the number of lateral roots were slightly higher than control (Fig. 2). The roots of the control plants were significantly longer (P value = 0.036) than those treated with the antagonistic strain. The results are summarized in (Table 2).

Growth of *T. afroharzianum* (TR04) under salt stress

Trichoderma afroharzianum TR04 was able to grow under salt stress conditions at 0.5 and 0.75M NaCl concentrations (Table 3). Additionally, the color of the colony significantly altered under salt stress. After 3 days, when sporulation has started, the colony was yellow, as opposed to the green color observed in the control (Fig. 3).

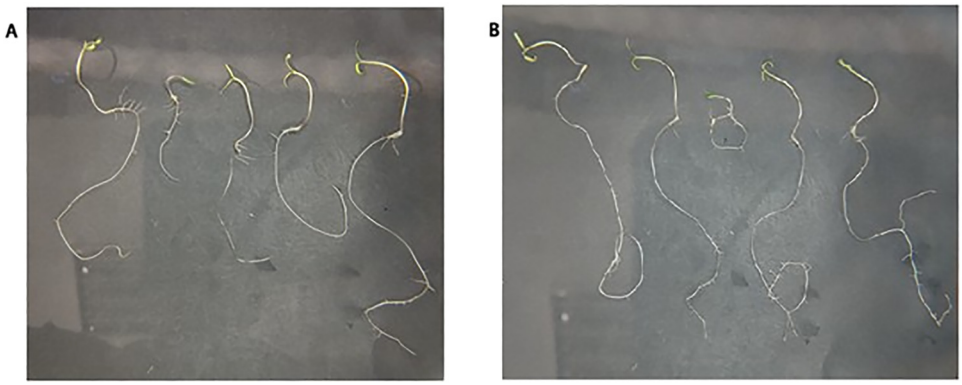

Fig. 2. Effect of *T. afroharzianum* (TR04) on tomato seedlings growth. (A) seedlings treated with *Trichoderma*, (B) control

Table 2. Effect of *T. afroharzianum* (TR04) on tomato seedlings growth

Evaluation	Growth (mm ± SD)		*P*-value
	Control	Treatment	
Root length (cm)*	14.20 ± 6.35[a]	10.92 ± 4.237[a]	0.1349
Root lateral (#count)	7.440 ± 4.407[a]	8.320 ± 3.945[a]	0.446
Shoot length (cm)*	3.428 ± 1.451[a]	3.136 ± 1.027[a]	0.1996
Fresh weight (g)	0.2619 ± 0.081[a]	0.2342 ± 0.047[a]	0.620

*A non-parametric Mann-Whitney *U* test was employed for comparison, as the data did not follow a normal distribution.

Table 3. Effect of NaCl concentration on the mycelial growth of *Trichoderma afroharzianum* (TR04) in PDA media

	Colony diameter (mm ± SD) **Growth inhibition (%)**			
	Control	0.5M (mm)	0.75M (mm)	1.25M (mm)
After 3 days*	84.4 ± 0.894[a]	51.0 ± 3.81[ab] **39.57**	35.00 ± 1.581[bc] **58.53**	0.00 ± 0.00[c] **100**
After 7 days*	90.00 ± 0.00[a]	84.40 ± 0.894[ab] **6.22**	82.6 ± 1.673[bc] **8.22**	37.80 ± 0.837[c] **58.00**

*A non-parametric Mann-Whitney *U* test was employed for comparison, as the data did not follow a normal distribution.

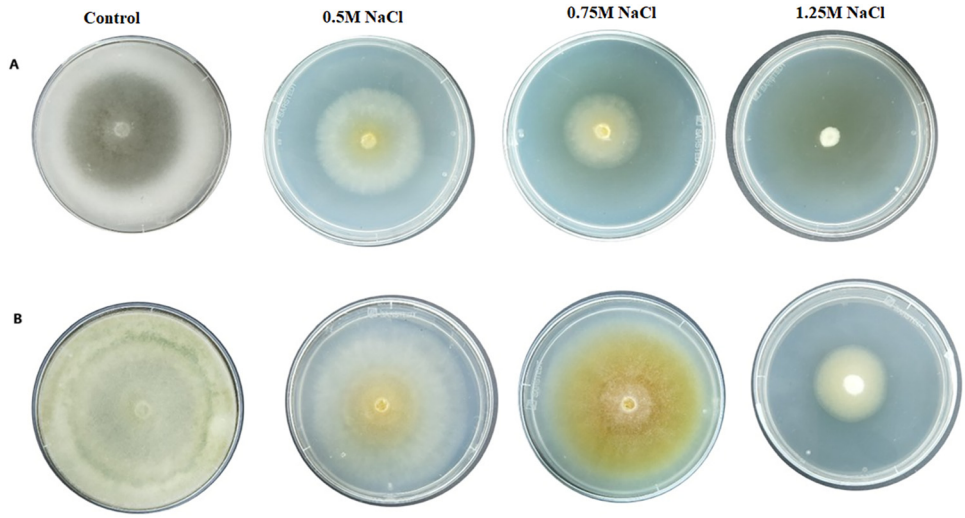

Fig. 3. Growth of *T. afroharzianum* (TR04) under salt stress. (A) 3 days, (B) 7 days

DISCUSSION

The number of *Trichoderma* species used in biocontrol has drastically increased in modern era (Yogalakshmi et al., 2021). Previous studies have demonstrated that *Trichoderma* species can be used as biocontrol (Zhang et al., 2015). *Trichoderma afroharzianum* (TR04) strain expressed a strong antagonistic effect against some Omomycota (*Aphanomyces cochlioides* and *Pythium acantophoron*) and Ascomycota (*Diaporthe eres, Eutypa lata, Neofusicoccum parvum* and *Botryosphaeria dothidea*) phytopathogens (Kovács et al., 2021) in dual culture antagonism assay. Additionally, studies showed that *Trichoderma* species employed versatile strategies to suppress other fungi and may rely on one or several "weapons" such as secretion of hydrolytic enzymes, secondaries metabolites, or both (Amaresan et al., 2022).

Understanding the antagonism mechanism is the first step towards in achieving the full potential of these biocontrol agents such as *Trichoderma* (Amaresan et al., 2022). The antagonistic effect related to the culture filtration (CFs) was significant but minimal with a 15.99% inhibition. This fact suggests that antibiosis is not the main mechanism of action, of the studied *T. afroharzianum* (TR04). These metabolites could be volatiles and non-volatiles, which hinder the colonization of pathogens (Meena et al., 2017). According to the results, the effects of volatiles and non-volatiles were significant. However, the effects were weak with 11.45% in non-volatile and 11.44% in volatile compounds. This observation strengthens the idea that antibiosis is not the main means of antagonism. According to Amaresan et al. (2022), *Trichoderma* possesses one or more mechanisms against plant pathogens, such as secreting hydrolytic enzymes and/or secondary metabolites, and importantly, they can also tolerate toxic metabolites from other fungi. Therefore, it is necessary to study the secretion of hydrolytic enzymes in order to understand the antagonist mechanisms from *T. afroharzianum* (TR04) for developing effective biological control strategies.

Globally, the tomato stands as a preeminent and extensively cultivated horticultural crop (Sehim et al., 2023). Prior studies have investigated how *Trichoderma* inoculation impacts the tomato root system during early growth (Rubio et al., 2014). It is well-know that *Trichoderma* can promote plant growth (Da Silva et al., 2020; Csótó et al., 2023). This effect is strain-dependent on the host plant (Amaresan et al., 2022). According to Tucci et al. (2011), the findings indicate that tomato genotype largely determines the extent of growth stimulation, suggesting that the response to *Trichoderma* spp. is genetically controlled.

Bioactive products of *Trichoderma* can induce profound changes in the plant phenotype as shoot development, root branching and cell differentiation for formation of root hours (Amaresan et al., 2022). Recent research has highlighted the potential of strains such as *Trichoderma asperellum*, which promote tomato seed germination by enhancing the number of leaves, shoot and root length (Sehim et al., 2023). This effect was similar with *Trichoderma paraseii* in tomato seeds germination even in salt stress (Rubio et al., 2014).

One of the primary modifications induced by *Trichoderma* strains in tomatoes is a change in root structure. Some fungi often lead to reduced primary root length while promoting lateral root development (Tucci et al., 2011). The result expresses a reduced primary root length, this result was similar to *Trichoderma atroviridae* and *T. virens* which stimulated lateral root and reduced primary root length (Contreras-Cornejo et al., 2009; Tucci et al., 2011). According to Tucci et al. (2011), this effect is due to the production of índole-3-acetic-acid. Although the number of lateral roots was not significantly different from the control, the treatment showed a higher mean number of lateral roots than the control. Therefore, the interaction between the fungi and the plant, including their mechanism and secondary metabolite secretion, could vary among strains (Amaresan et al., 2022).

Regarding salt tolerance, our findings are consistent with those of Liu et al. (2023). Their *Trichoderma* strains, characterized by salt tolerance, exhibited growth between 2 and 4% NaCl. This parallels our results, where growth was observed on PDA at 0.5M (~2.9%) and 0.75M (~4.4%) NaCl concentrations within the initial three days. Regarding the color of *Trichoderma* spores, a dramatic change was observed, primarily to yellow, consistent with the findings of Liu et al. (2023). According to Zhang et al. (2021), yellow pigmentation is linked to conidiation, cell wall integrity, and stress tolerance. This effect is due to PKS genes (Zhang et al., 2021), which are involved in the production of metabolites known as polyketides

(Reino et al., 2008). These metabolites are considered antifungal compounds (Reino et al., 2008). After 7 days, *T. afroharzianum* (TR04) could grow in 1.25M NaCl, and the color was mostly white, consistent with the findings of Liu et al. (2023). Therefore, its ability to grow under saline conditions suggests its potential for use in high-salinity environments, which could be beneficial for improving crops in saline soils.

In conclusion, the *T. afroharzianum* (TR04) strain demonstrated significant efficacy as a biocontrol agent against *B. cinerea*, as evidenced by dual culture tests (Zabiák et al., 2025). Regarding its antagonistic mechanisms, our findings suggest that the production of antifungal compounds is not the primary mechanism, indicated by a relatively low, yet significant, inhibition effect of 15.99%. Furthermore, applying *T. afroharzianum* (TR04) to tomato seeds reduced primary root length, a response similar to that observed with *Trichoderma atroviride* and *Trichoderma virens*. Additionally, *T. afroharzianum* (TR04) exhibited remarkable salt tolerance, growing even in 1.25M NaCl.

Conflicts of interest: Erzsébet Sándor receives a royalty for the Trichoderma product containing *T. afroharzianum* TR04 tested in this study. The rest of the authors declare no conflicts of interest.

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