Arbuscular mycorrhizae induce resistance against Fusarium wilt in onion in Boyacá, Colombia

Micorrizas arbusculares inducen la resistencia contra fusariosis en cebolla en Boyacá, Colombia

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ABSTRACT

Bulb onion (*Allium cepa* L.) is a globally consumed vegetable, and as the global population increases, demand for this crop is continuously rising. Unfortunately, production is significantly reduced—up to 40%—due to Fusarium wilt, a fungal disease caused by the *Fusarium* genus. In Boyacá, Colombia, one of the central onion-producing regions, chemical control is the primary method for controlling this disease despite the negative impact of chemicals on soil health and their decreasing efficacy. One alternative management strategy is resistance induction through microorganisms, which has been tested with the *Trichoderma* genus but not with native populations of arbuscular mycorrhizal fungi (AMF). This study aims to evaluate the resistance-inducing effect of a consortium of native AMF from Boyacá on the bulb onion. *Fusarium oxysporum* pathogens and native AMF were isolated from *A. cepa* L. crops in Boyacá and tested under greenhouse conditions for 18 weeks in a completely randomized design. The study evaluated the effects of the pathogen and AMF consortium on leaf number, average leaf area, and bulb growth. It found resistance-induction and growth promotion effects, as well as the adverse effects of the pathogen and the combined effects of both microorganisms. The findings suggest that native AMF consortia from Boyacá exerted a protective impact against Fusarium wilt, improving plant productivity under sterile soil conditions.

Keywords: infection prevention, inoculation time, mycorrhizal consortium, sanitary status.

RESUMEN

La cebolla de bulbo (*Allium cepa* L.) es una hortaliza consumida a nivel global y con el crecimiento poblacional mundial su demanda se hace cada vez más grande. Desafortunadamente su producción disminuye hasta un 40% debido a la fusariosis, enfermedad causada por hongos del género *Fusarium*. En Boyacá, Colombia, una de las principales regiones productoras de cebolla, el control químico es el principal método contra esta enfermedad, aunque presenta impactos negativos en la salud del suelo y su eficacia ha disminuido. Una de las alternativas de manejo es la resistencia inducida por microorganismos, como se ha probado con hongos del género *Trichoderma*, pero no con poblaciones nativas de hongos micorrízicos arbusculares (HMA). El objeto del presente trabajo fue evaluar el efecto inductor de resistencia a la fusariosis utilizando un consorcio de HMA nativos de Boyacá en cebolla de bulbo. Se realizaron aislamientos del patógeno *Fusarium oxysporum* y de HMA a partir de cultivos de *A. cepa* L. nativos de Boyacá y, se realizaron pruebas en condiciones de invernadero durante 18 semanas con un diseño completamente al azar. Se evaluaron los efectos del patógeno y del consorcio de HMA sobre el número de hojas, el área foliar promedio y el crecimiento del bulbo. Se encontraron efectos de inducción de resistencia y de promoción de crecimiento; también se observaron los efectos adversos del patógeno, así como efectos conjuntos de ambos tipos de microorganismos. Se concluyó que los consorcios de HMA de Boyacá promovieron un efecto protector contra la fusariosis, mejorando la productividad de la planta en condiciones de esterilidad del suelo.

Palabras clave: prevención de infección, tiempo de inoculación, consorcio micorrízico, estado sanitario.

Introduction

The global human population reached 8,000 million in 2022 and is expected to increase to 9,000 million by 2050 (ONU, 2019; 2022), requiring more efficient food production. Intensive agriculture and chemical inputs have increased the prevalence of diseases and insect pests while negatively impacting soil microbiota (Rojas Rodríguez & Ortuño, 2007). This, along with acquired resistance to some pathogens, highlights the need to explore mechanisms aligned with natural dynamics (Islam *et al*., 2024; Yin *et al*., 2023).

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Boyacá leads onion production in Colombia, accounting for 41% of the total output with 260,970 t in 2023 (MinAgricultura, 2024). Colombia's bulb onion production systems operate within diverse biophysical, socio-ecosystem, and socioeconomic environments. Despite this variability, they can sustain and strengthen their supply, ensuring a steady provision for local and national markets throughout the year. However, they are impacted by imports from neighboring countries.

Worldwide, *Fusarium* species are the primary fungal soil pathogens affecting onion crops (Delgado-Ortiz *et al*., 2016; Montes-Belmont *et al*., 2003), leading to Fusarium wilt. It is essential to note that the plant's phenological stage can increase susceptibility to pathogens; the susceptibility can be increased or reduced in mature or nursery plants (Frare *et al*., 2019). In onion bulbs, *Fusarium* spp. fungi can initially cause leaf yellowing, followed by wilting, leaf curling, rot, root breakage, and eventually plant death (Gardezi *et al*., 2001; Martínez-Salgado *et al*., 2021). If infection occurs late, symptoms may not appear until storage (Cramer, 2000).

Economically significant *Fusarium* species include *F. proliferatum, F. solani*, and *F. oxysporum*, which can reduce crop yields by up to 40% (Betancourth García *et al*., 2020; Martínez-Salgado *et al*., 2021). Fusarium wilt control in onion crops heavily relies on chemical inputs (Naeini *et al*., 2010; Navarro *et al*., 2021; Vergel *et al*., 2016), overlooking alternatives like biological control with *Trichoderma* spp. (Delgado-Oramas, 2020), endophytes (Abdelrahman *et al*., 2016), resistance induction by extracts or microorganisms (Fontana *et al*., 2021), and exposure to UV radiation (Winona *et al*., 2025).

Among the three plant defense mechanisms—physical, chemical, and induced (Couto & Zipfel, 2016)—plants activate induced responses when they detect pathogen-associated molecules, triggering pattern-induced resistance. In response to specific microbial effectors, this leads to effector-triggered immunity or acquired resistance, often resulting in the hypersensitive response characterized by localized cell death (Jones & Dangl, 2006).

In recent decades, interest in using arbuscular mycorrhizal fungi (AMF) for food production and plant disease control has increased (Whipps, 2004). AMF are microorganisms that play a crucial role in plant-associated biological processes, enhancing growth, yields, and biochemical components that strengthen defense capacities against pathogens such as fungi and bacteria (Amin & Ahmed, 2023; Błaszczyk *et al*., 2014). Plants respond favorably to AMF interactions, improving growth and increasing resistance to abiotic stressors such as drought, temperature fluctuations, salinity, heavy metal toxicity, and nutrient deficiency or excess (Datta & Kulkarni, 2012; Gardezi *et al*., 2001; Rivera Méndez *et al*., 2014; Wilches Ortiz *et al*., 2019).

The AMF also contribute to maintaining the structural stability of soils, whether in forest or crop conditions, by secreting glomalin, mucilages, and hydrophobins through their hyphae: these contribute to soil aggregation (Rashid *et al*., 2016) by generating hyphal networks that trap and bind soil particles, providing cohesion to the particles and stability to the aggregates (Leifheit *et al*., 2014; Schütz *et al*., 2022). The inductive defense effect of arbuscular mycorrhizal fungi is recognized in plants such as *Elymus nutans* (Zhang *et al*., 2022), *Solanum lycopersicum* (Badrbani *et al*., 2024; Saha *et al*., 2022), *Plantago lanceolata* (Qu *et al*., 2021), and other plant species such as *Poncirus trifoliata* (Liu *et al*., *2024*) and *Zea mays* (Hao *et al*., 2012). This mechanism is used to control plant pathogens (Dey & Ghosh, 2022). The defensive effect of AMF extends beyond the root level. These fungi also mediate in the control of fungal foliar diseases (Kashyap *et al*., 2024). Plant defenses are induced not only by arbuscular mycorrhizal fungi but also by an adequate supply of nutrients (Stratton *et al*., 2022).

Regarding bulb onions, there are positive references. Agudelo Becerra and Casierra-Posada (2004) find that undefined AMF in field conditions increase resistance to *F. oxysporum*, inhibiting pathogen growth, reducing bulb damage, and mitigating salinity effects; after that, Jaime *et al*. (2008) report a reduction of about 50% in the incidence of white rot in field conditions using *Glomus intraradices*. Yağmur *et al*. (2024) found up to a 73% reduction in the severity of basal wilt expression using *Funneliformis mosseae* against *F. oxysporum* in greenhouse conditions. Studies on *Rhizophagus irregularis*-inoculated *A. cepa* crops demonstrate positive effects on growth, quality, and yields, driven by increased chlorophyll content and improved nutritional properties (El-Sherbeny *et al*., 2022; Rozpądek *et al*., 2016). However, Ghanbarzadeh *et al*. (2016) report that the simultaneous inoculation with *F. mosseae* and *T. harzianum* stimulated onion growth but partially inhibited *F. mosseae* colonization.

When evaluating antagonistic or suppressive effects against pathogens, an important aspect is the concentration at which the pathogen induces disease symptoms. Generally, the increase in *F. oxysporum* concentration is directly correlated to the severity of the symptoms. For example, in cotton (*Gossypium hirsutum*), wilt symptoms and reductions

in plant growth occur at soil inoculum levels of 10^3 conidia and become more severe at 10^4 conidia/g and higher (Hao *et al*., 2009). In Mexican lime (*Citrus* x *aurantifolia*), severity steadily increases as microconidia density rose from 500 to 8000 per g of soil (Morgan & Timmer, 1984). In chickpea (*Cicer arietinum*), maximum disease intensity is observed at chlamydospore densities as low as 6 to 50 per g of soil, depending on the race of *F. oxysporum* (Navas-Cortés *et al*., 2007). Similarly, in watermelon (*Citrullus lanatus*), wilt incidence is strongly linked to inoculum densities ranging from 100 to 1200 CFU/g (Zhou & Everts, 2003).

Even in the indirect transmission of the pathogen, such as laurel wilt in avocado, caused by the fungus *Raffaelea lauricola* and transmitted by the exotic ambrosia beetle *Xyleborus glabratus,* symptom severity is lower at 10^2 than at higher concentrations, and both 10^2 and 10^3 conidia cause less disease than 10^4 and 10^5 (Hughes *et al*., 2015).

Evaluating the interactions of native AMF consortia in *A. cepa* crops helps expand the field research on sustainable alternative onion production. This study posited: (1) that pathogen concentration does not influence the severity of fusariosis in *A. cepa*, and (2) that AMF provided a protective effect against Fusarium wilt, enhancing plant productivity. The study tested for differences among treatments with varying pathogen concentrations. It established whether AMF-inoculated plants exhibited better growth and productivity.

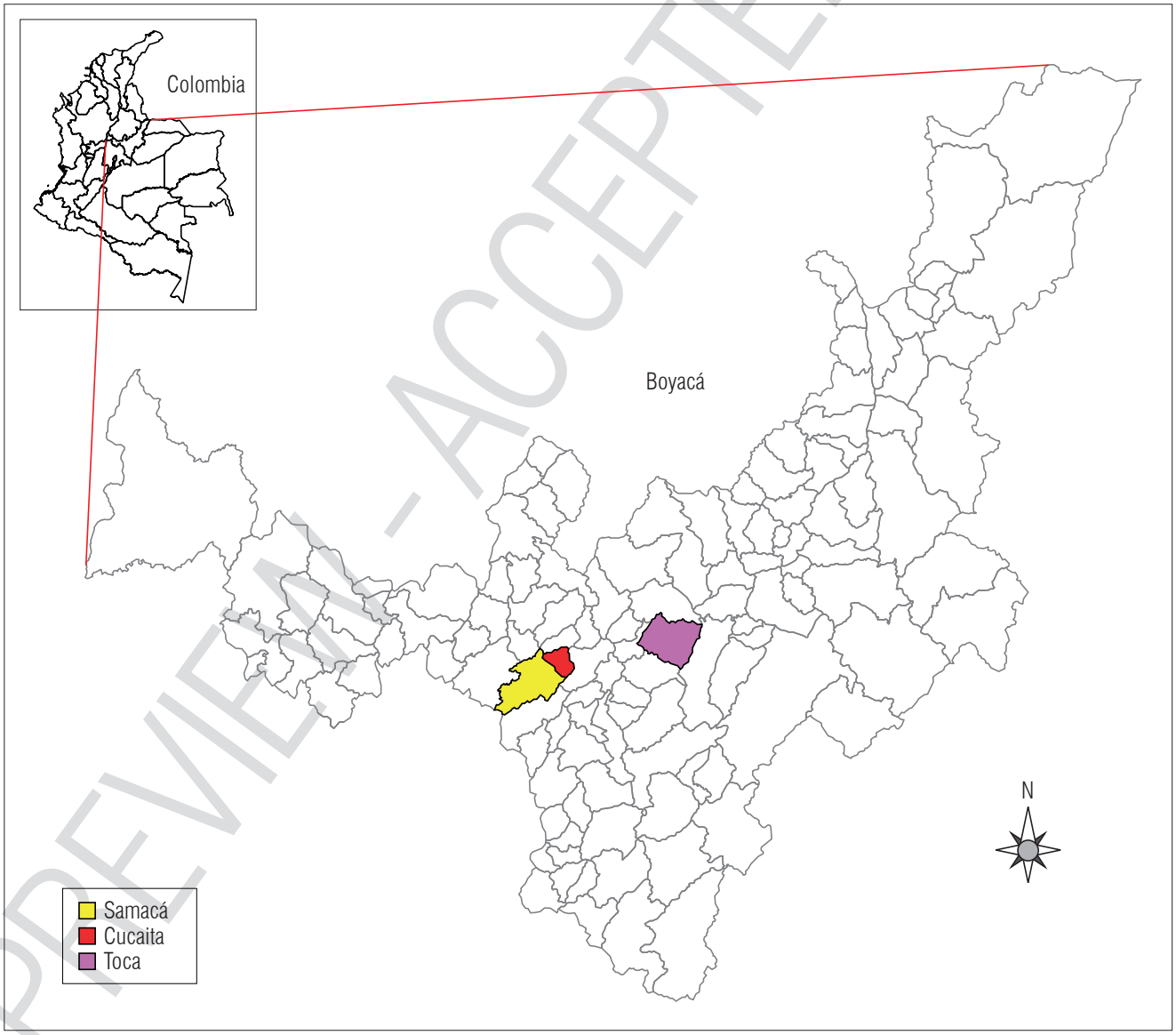

FIGURE 1. Sampling sites in the municipalities of Cucaita, Toca, and Samacá in Boyacá, Colombia.

Materials and methods

Sampling

Samples were collected in 2022 from three municipalities in Boyacá—Cucaita, Toca, and Samacá—at elevations ranging from 2,641 to 2,838 m a.s.l. Two farms growing onions were chosen in each municipality. Ten random top-soil subsamples were taken from each farm and combined to yield approximately 1,000 g of soil (Fig. 1). Additionally, onions in the bulb thickening phenological phase, showing Fusarium wilt symptoms were collected. All samples were stored in labeled plastic bags and kept refrigerated until processed at the Zenkinoko SAS laboratory in Cucaita.

Extraction of AMF spores

The AMF spores were extracted by wet sieving and decantation following Sieverding (1984). Ten grams of soil were processed through a series of mesh sieves with openings of 2000, 500, 250, 120, and 45 µm. The material retained in the smaller sieves was subjected to sucrose gradient centrifugation (70-80%). The spores were examined using a ZEISS Stemi 305 stereomicroscope. They were subsequently extracted with a syringe fitted with a yellow micropipette tip and stored in refrigeration at 2-4°C in 2 ml conical tubes containing 100 µl of distilled water, at a rate of 40 spores per tube. For experiments, only the three most abundant species were selected.

Only spores that appeared viable (based on visual assessment and the presence of cytoplasmic content), not parasitized, broken, or perforated, were selected. Morphospecies or higher taxonomic classification was determined based on morphological characteristics, including spore and hyphal coloration, presence or absence of a shield, number of walls and layers, shape and attachment of the subtending hypha, presence, absence, and position of the septum, presence of scars, presence of a sacculus, ornamentation, whether spores were solitary or clustered, the type of aggregation, and reaction to Melzer's reagent. Genus-level identification was performed according to the existing literature. Species-level identification was conducted where possible by comparing morphological traits with data from the International Culture Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi (INVAM) (https://invam.wvu.edu), Professor Sidney Stürmer's collection (https://sites.google.com/site/cicgfma/home), and Professor Janusz Blaszkowski's Glomeromycota collection (http://www.zor.zut.edu.pl) (Blaszkowski, 2012), as well as recently described species up to December 2023.

Isolation of *Fusarium* spp. strains

The isolation of *Fusarium* spp. followed the methodology described by Hernández *et al*. (2019). Onion root segments (~2 cm) from sick plants were cleaned with distilled water to remove soil residues, surface-sterilized with 2% sodium hypochlorite for three minutes, rinsed with distilled water, immersed in 70% ethanol for one minute, and subsequently rewashed with distilled water. The roots were dried on filter paper and plated (4 fragments per Petri dish) on potato dextrose agar (PDA) without antibiotics or antimycotics. A total of 40 plates were incubated at 28°C until visible colonies appeared, within 1 week.

Of 57 colonies obtained, the 20 that exhibited cotton-like growth and characteristic pink, red, or white *Fusarium* pigmentation (Duarte *et al*., 2016) were selected. Using a mycological loop, mycelial tip fragments were subcultured onto PDA by puncture and incubated at 28°C for 7 d. Among these, 15 purified *Fusarium* spp. strains were retained for further identification. To preserve isolates, mycelial fragments were transferred to inclined agar tubes (Montesinos *et al*., 2015), incubated at 28°C for 7 d, and stored at 4°C.

Identification of *Fusarium* spp.

For *Fusarium* species identification, carnation leaf agar (CLA) at 2% was used to promote the formation of both macroconidia and microconidia (Duarte *et al*., 2016). Autoclaved carnation leaves (in five fragments) were added to 2% water agar and refrigerated for one day at 4°C. The 15 fungal isolates were inoculated by puncture and incubated at 28°C for 7 d. Conidial observations were conducted using traditional slide mounts, employing a mycological handle, a lactophenol blue stain, and a Primo Star ZEISS microscope, following the species descriptions of Leslie and Summerell (2006).

Fusarium spp. inoculum mass-production

The previously identified strains were tested for growth rate in PDA at 28°C, and the two isolates with the highest growth rate were selected for assays. For pathogen mass production, the methodology of Jarek *et al*. (2018) was followed. A test tube containing the isolate was supplemented with 1 ml of sterile distilled water and a drop of Tween 80. The fungal mycelium was scraped from the medium using a round inoculation handle and transferred to another tube. A 100 µl aliquot of the suspension was spread onto PDA plates using a Drigalski spatula in a spiral pattern. Five replicates were prepared and incubated at 28°C for 7 d.

Onion seed sowing

Sterilized peat (2 kg, autoclaved at 121°C for 1 h) was used as a substrate and placed in 72-cavity germination trays, which were isolated from the soil surface by a plastic-covered table. Onion seeds were surface-treated with 2% sodium hypochlorite for 1 min, followed by three rinses with distilled water. Then, using surface-sterile forceps, two seeds were sown in each tray cavity.

One month after germination, seedlings were transplanted into pots containing a mixed substrate (1:1 soil: sand) that had been double-sterilized in an autoclave at 121°C for 1 h. The peat substrate was gently removed from the roots with a spatula to minimize damage during transplant. Depending on the treatment, the fungal pathogen, the AMF, or both were placed in the center of the pot before transplanting the seedlings. Each pot contained a single seedling, and additional substrate was added to cover the roots without burying the foliage.

Experimental design

A completely randomized design was used with six treatments and ten plants per treatment (five per dosage), resulting in a total of 60 plants. The inhibitory effect of AMF on *Fusarium*-induced disease was evaluated based on bulb growth (mm), leaf length average (cm), and leaf count over 18 weeks. The treatments were performed as in Table 1.

TABLE 1. *Fusarium* and arbuscular mycorrhiza inoculation treatments on *A. cepa* plants in greenhouse conditions.

Treatment	AMF	*Fusarium*	Time of inoculation
T0	-	-	-
T1	x	-	Initial
T2	-	x	Initial
T3	x	x	*Fusarium* 7 d after AMF
T4	x	x	AMF 7 d after *Fusarium*
T5	x	x	Initial and simultaneous

Conventions: - = No inoculation, x = inoculation.

Three fertilization events were conducted using a 13-40-13 (NPK) formulation, following standard fertilization schedules for the onion crop. Additionally, plant mortality due to disease and phenotypic traits such as chlorosis and wilting was recorded.

For AMF inoculation, 250 µl of distilled water was added to each conical tube containing 40 AMF spores. Each tube suspension was then applied directly onto the roots per pot using a micropipette under a stereomicroscope, ensuring proper adhesion of the spores to the root surface. For *Fusarium* inoculation, mass culture conidia suspensions were adjusted to 1×10^8 conidia ml^{-1} using a Neubauer chamber. According to the treatment, two pathogens at both concentrations (75 µl and 420 µl) were applied directly to the roots, along with a control without conidia. Five plants per concentration were used per *Fusarium* treatment.

Data analysis

Normality and homoscedasticity tests were performed before statistical analysis. All analyses were conducted using SPSS v.27. Figures were generated with SigmaPlot v.12. A two-way ANOVA (weeks and pathogen concentration) was performed to assess the effect of *Fusarium* concentration (0, 75, 420 µl) on the evaluated variables and whether differences persisted over time. A post hoc Bonferroni test was applied at a 5% significance level if significant differences were detected.

A two-way ANOVA (weeks and treatment) was conducted to evaluate differences among AMF and *Fusarium* treatments over time. When significant differences were observed, a post-hoc Bonferroni test was applied (5% significance level). The interaction between time and treatment effects was also analyzed to determine the persistence of treatment effects over time.

Results

On each farm, 7 to 16 arbuscular mycorrhizal fungal species were identified, with the three most abundant being *Racocetra* sp., *Acaulospora* sp., and *Acaulospora morrowiae*, which were used in the consortium. Meanwhile, the phytopathogenic fungus used in the experiment corresponds to *Fusarium oxysporum* Schltdl.

We observed that the two pathogen concentrations did not differ in their effects on bulb growth and leaf number. However, significant differences arose when comparing these concentrations with those in the treatment in which the pathogen was absent from the soil. Additionally, no interactions between concentrations and time were detected (Fig. 2A and B).

However, when evaluating the interaction between average leaf length and the week of evaluation, a differential effect of *Fusarium* strain concentration was observed, where the absence of the pathogen resulted in shorter leaves. In the treatment inoculated exclusively with the AMF consortium, a differential resource allocation effect was observed, where plants allocate more carbon to the mycorrhizal symbiosis and root development (Smith & Read,

2008; Zheng *et al*., 2015). This finding is consistent with previous observations (Jakobsen *et al*., 2003; Smith *et al*., 2009), and that AMF colonization can temporarily reduce shoot growth while the hyphal network is established and the root system is reinforced. Moreover, concentration interaction was detected only at the 17th week (Fig. 2C).

Leaf number increased precisely at the onset of bulb thickening (approximately at week 7), whereas the average leaf length did not follow the same trend; nevertheless, the mycorrhizal inoculation generally resulted in greater bulb diameter, leaf number, and leaf length than any other treatment (Fig. 3).

Although mycorrhizal and *Fusarium* inoculation did not exhibit an overall protective effect across treatments, after 18 weeks, bulb diameter and leaf number were similar among treatments with mycorrhizae and those where *Fusarium* and mycorrhizae were applied simultaneously (Fig. 3A and B).

Leaf number was significantly higher during the first 10 weeks following mycorrhizal application alone, a level that was eventually reached by the mycorrhizae + *Fusarium* treatment at 11 weeks (Fig. 3B). The treatment with AMF alone showed a gradual decrease in foliar parameters that became more noticeable as bulb size increased, and its behavior was similar to that of other therapies; however, in the last week, it showed an abrupt increase. Apparently, when *A. cepa* is inoculated only with AMF, without any other microorganism, physiological responses are faster and more pronounced during this final period (Fig. 3B and C).

Between weeks 16 and 17, a decline in both leaf number and length was observed across all treatments. In contrast, no such increase in bulb thickness was observed. This suggested a possible redistribution of energy resources toward the bulb rather than maintaining the photosynthetic area. Before this decline, an increase in average leaf length followed a consistent trend over time, progressing more rapidly in the control treatment than in the arbuscular mycorrhizae treatment, and finally in the simultaneous mycorrhizae + *Fusarium* treatment, compared to other treatments. However, this increase was followed by a subsequent decline after reaching its peak (Fig. 3C).

Treatments 2 (*Fusarium* sp.) and 4 (*Fusarium* sp. day 1 + Mycorrhizae day 7) lost one sample unit by week 5 due to the pathogenic fungus. Additionally, these treatments, along with treatment 3 (Mycorrhizae day 1 + *Fusarium* sp. day 7), exhibited symptoms of illness, such as progressive leaf chlorosis after 12 weeks.

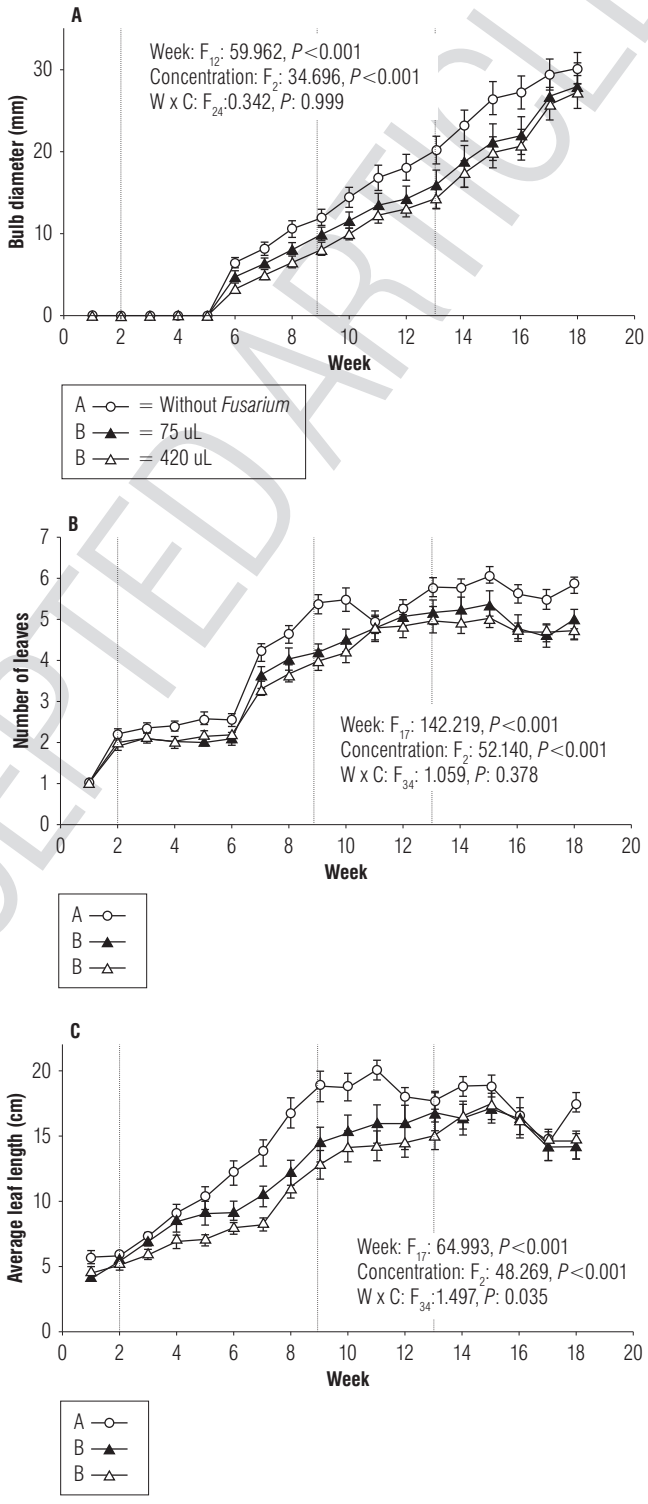

FIGURE 2. Effect of *Fusarium* sp. strain concentration on growth parameters and productivity of bulb onion (*A. cepa*) over 18 weeks. Bars correspond to the standard error. A) Bulb diameter, B) number of leaves, C) average leaf length. Uppercase letters within the labels correspond to the Bonferroni post hoc test for each strain concentration in each evaluated variable. The vertical dotted lines indicate fertilization events.

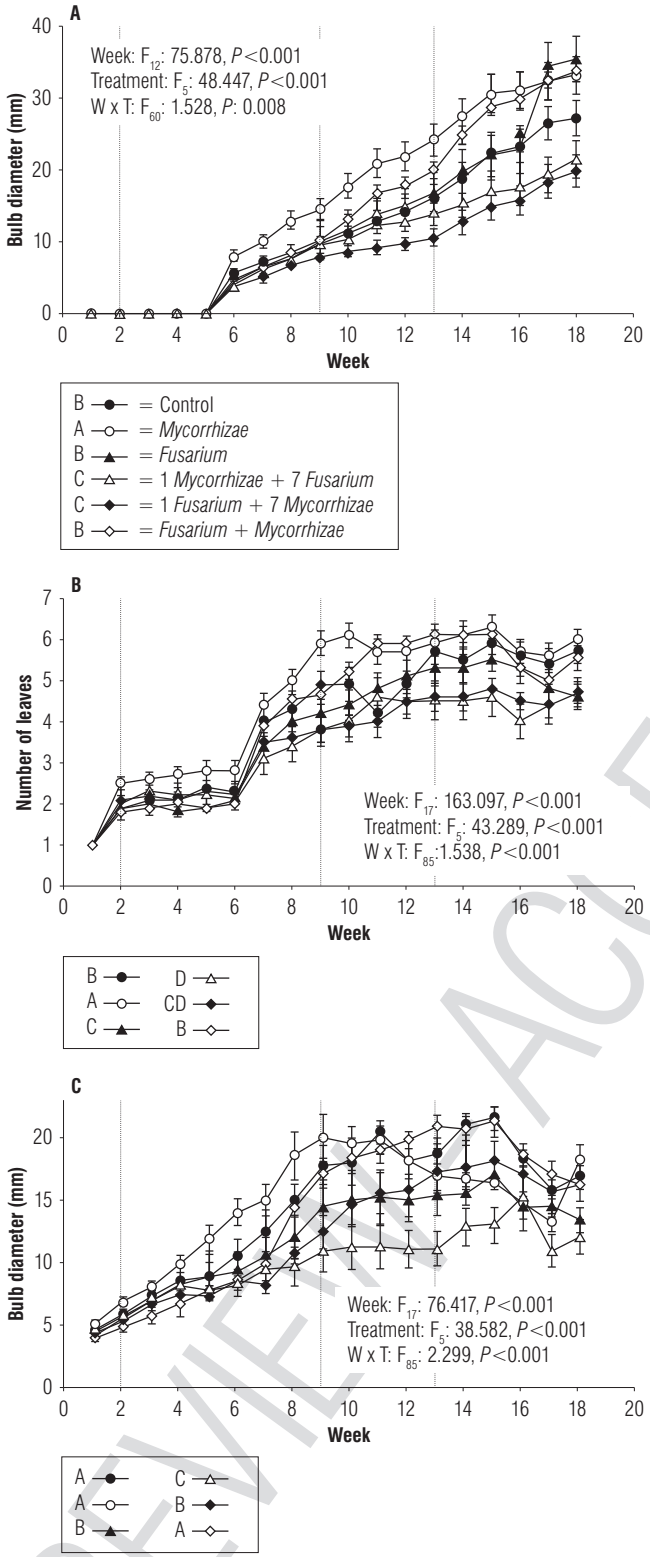

FIGURE 3. Effect of *Fusarium* sp. and arbuscular mycorrhizal treatments on bulb onion (*A. cepa*) growth parameters and the productivity over 18 weeks. Bars correspond to the standard error. A) Bulb diameter, B) number of leaves, C) average leaf length. Uppercase letters within the labels correspond to the Bonferroni post-hoc test for each strain treatment in each evaluated variable. The vertical dotted lines indicate fertilization events.

Discussion

Previous studies related to some AMF, such as *Glomus*, *Rhizophagus*, and *Funneliformis*, show effects against *F. oxysporum* wilt in onion. However, only Hu *et al.* (2010) and Tanwar *et al.* (2013) report the positive impact of *Acaulospora* spp against this disease. Evidence for *Racocetra* remains scarce and seems to be associated with mixed-species inoculum rather than effects specific to the genus.

There is a wide range of experiments aimed at reducing the impact of *Fusarium* spp. on different crops, including onions. These range from the use of one single antagonistic species, the use of known bacteria, fungi, or both groups of organisms in a synthetic consortium (such as the present), to the use of amendments (Habte & Dobo, 2025), plant extracts (Hegazy *et al*., 2024), or the use of undefined microorganism mixtures as in efficient microorganisms (Guigui *et al*., 2024). In the last-mentioned, the authors explore the antagonistic, suppressive, or resistance-inducing effects of products with different attributed properties, such that the set of components (in most cases undefined) can, simply or synergistically, contribute to controlling pathogenic microorganisms.

This study tested two hypotheses. The first proposed that pathogen concentration influences the level of Fusarium wilt severity in *A. cepa* plants, requiring an individual analysis of the evaluated parameters. Regarding bulb size and leaf number, all treatments inoculated with *F. oxysporum* showed similar averages over time regardless of pathogen concentration (Fig. 2A and B). All *F. oxysporum*-inoculated treatments displayed chlorosis and wilting symptoms, with two treatments also showing plant mortality (one at 75 µl and another at 420 µl). This indicated that *Fusarium* sp. concentrations did not significantly differ in their effect on Fusarium wilt severity, as assessed by measuring bulb size and leaf number. Both concentrations used likely exceeded the unknown minimum infectious dose of *F. oxysporum* for *A. cepa*, as evidenced by the appearance of disease symptoms. Similar results are reported by Manasa *et al.* (2017) working with carnations. Consequently, increasing the concentration does not significantly affect disease severity (Biswal *et al*., 2020; Wright *et al*., 1997) when evaluating by leaf number or bulb diameter.

For leaf length, an inverse relationship was observed between pathogen concentration and average leaf length, suggesting that pathogen concentration affects the plant's photosynthetic capacity. However, this effect was mitigated after 14 weeks, when the leaf length reached its maximum

average in infected plants (Fig. 2C). Several authors have reported the severity of different *Fusarium* species in various crops, such as bean (*Phaseolus vulgaris*), where it affects plant growth and development (Biswal *et al*., 2020), or soybean (*Glycine max*), where it reduces productivity without significantly affecting other variables (Freitas *et al*., 2016).

Regarding the second hypothesis, because *F. oxysporum* concentration did not affect leaf number or bulb diameter (key productivity variables), all treatments were considered independent units, regardless of pathogen concentration. It was hypothesized that arbuscular mycorrhizal fungi promote a protective effect against Fusarium wilt, thereby enhancing the plant's productive characteristics—a detail that warrants close examination.

When comparing the simultaneous application of both microorganisms to the control (neither *Fusarium* sp. nor mycorrhizae) and considering that both outperformed *F. oxysporum* treatment alone in foliar measurements, a protective effect against the pathogen could be observed (Fig. 2B and C). Similar results are reported in *Citrullus* sp., where *Trichoderma viride* effectively suppressed *F. oxysporum* in *Solanum lycopersicum* plants (Ponsankar *et al*., 2023). Additionally, biocontrol effects of *Trichoderma harzianum* and *Glomus mosseae* against basal rot in onion plants (Ghanbarzadeh *et al*., 2016) are well documented. Comparing the control to the mycorrhiza-only treatment revealed a stimulatory effect of mycorrhizae on both leaf number and bulb diameter (Fig. 3A and B). This effect is widely recognized in crop plants associated with arbuscular mycorrhizal fungi (AMF), such as oat (*Avena sativa*) (Flores-Juárez *et al*., 2020) and banana (*Musa* sp.) (Bernal, 2020), among other commercially relevant species. Furthermore, onions fertilized with arbuscular mycorrhizal fungi have been reported to produce a higher quantity of indigestible oligosaccharides, which may be linked to protective mechanisms or potential medical applications (Lone *et al*., 2015).

However, the combined use of pathogenic and beneficial fungi reduced the individual effects of both microorganisms on the plant. While pathogen severity was minimized, productivity levels took longer to reach those observed with mycorrhizae alone. This represents a trade-off in protective benefit (Delgado-Oramas, 2020) and reflects the energetic balance between production and defensive processes (Cipollini & Heil, 2010; García *et al*., 2021). A similar trend was observed for average leaf length, with the effect becoming evident primarily after eight weeks of treatment (Fig. 2C). Interestingly, although average leaf length decreased first in the mycorrhiza treatment (week 12), this pattern was subsequently observed in the combined biological treatments and the control (week 16), once maximum average values were reached and, while leaf length declined, bulb diameter continued to increase (Fig. 3). This source-sink redistribution of nutrients, in which leaves act as sources and bulbs as sinks, is a common phenomenon across vegetation (Azcón-Bieto & Talón, 2013), particularly in short-cycle species like bulb onion once phenological maturity is reached. What makes this particularly interesting is that the maximum average leaf areas and the timing of their attainment appear to be closely linked to plant health status, being early in healthy plants and late in sick plants (Fig. 3B and C).

Finally, the staggered inoculation treatment—applying the mycorrhizal consortia first, followed by *F. oxysporum* —produced unexpected results, yielding the lowest productivity across all evaluated variables, even lower than *F. oxysporum* alone (Fig. 3). This suggested a greater metabolic burden that negatively impacted plant development. These findings indicated that mycorrhizal application should be performed preventively in pots rather than as a curative measure once *F. oxysporum* wilt has been established.

According to the results of this experiment, the best time to apply native arbuscular mycorrhizal fungi in onion crops is at the seedling stage, when the plants are developing their first roots, and in sterile soil conditions, without fertilizer, until the relationship between both members is established. In this way, the AMF application enhances productivity and provides protection against Fusarium wilt. Considering the potential of these AMF consortia to protect against *F. oxysporum*, it is essential to evaluate their impact on other *Fusarium* species that affect *A. cepa*. Moreover, further research is needed to determine their effectiveness in non-sterile conditions, where similar outcomes are expected due to the presence of the most abundant native AMF.

Conclusions

Under greenhouse sterile soil conditions, pathogen concentration did not significantly affect bulb growth or leaf number, but it negatively affected leaf length. The protective effect observed in onion plants inoculated with native AMF consortia (*Acaulospora* spp. and *Racocetra* sp.) from Boyacá supports their role in mitigating *F. oxysporum* wilt. This is the first report of *Racocetra* in consortia with other AMF as a biological control agent.

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Conflict of interest statement

The authors declare that there is no conflict of interests regarding the publication of this article.

Author's contributions

RHP and SSS designed the experiment; SSS conducted the field and laboratory experiments; RHP and CJR contributed to data analysis; RHP, CJR, and SSS wrote the draft of the manuscript. All authors reviewed the final version of the manuscript.

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