

Article

The Origin and Type of Inoculum Determine the Effect of Arbuscular Mycorrhizal Fungi on Tomato under Different Irrigation Regimes

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Abstract: Arbuscular mycorrhizal fungi (AMF) play a crucial role in the resilience of plants subjected to water deficit. The objective of this study was to evaluate the impact of AMF from a semi-arid and humid ecosystem, applied as inocula (two monospecific and two consortia), and three irrigation doses (100%, 85%, and 70%) on tomato plant growth. A factorial experiment in a completely randomized design was used. Colonization with monospecific inocula (EH and ES) showed contrasting differences at 85% and 100% irrigation rates. With gradually increasing irrigation rates, colonization decreased with the CH consortium, while the CS consortium showed similar colonization levels at all three irrigation rates. AMF from humid environments (monospecific or in a consortium) did not affect equatorial diameter when the irrigation rate was reduced by 15%, while polar diameter was similar at all three irrigation rates. Inocula from the semi-arid ecosystem promoted the greatest equatorial and polar diameters at the 100% irrigation dose. The monospecific inoculum of *C. etunicatum* (ES) showed great potential to promote plant growth and development at the 100% irrigation dose and could be a biotechnological tool to improve tomato yield under conditions similar to those of this study.

Keywords: consortia; species; irrigation; mycorrhizae; tomato



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1. Introduction

Arbuscular mycorrhizal fungi (AMF) form a mutualistic symbiosis with most plant species [1]. They are found in almost all soils and are of vital importance in reducing plant water and nutritional stress [2–4]. In this symbiosis, the plant contributes the by-products of the photosynthesis process to AMF [5]. These fungi act in soils as natural biofertilizers, and their absence can affect ecosystem functioning [6]. Symbiosis depends on several factors, such as the soil, plant, and environment [1], and their use can help increase crop yields [6–8], protect against soil pathogen attacks [9], and provide tolerance to heavy metal contamination [10].

Water availability and food security are challenges to be considered due to their vulnerability to climate change [11]. Climate change is causing alterations in the interactions between plants and soil organisms, which is modifying ecosystems and affecting their functionality. In this context, AMF could contribute to plant adaptation to climate change by reducing the extinction of some plant species and allowing host plants to adapt to new soil ecosystems. However, some types of mycorrhizal fungi may vary in their responses to climate change. Research indicates that ectomycorrhizal fungi are more variable in their response than arbuscular mycorrhizal fungi to global warming [12].

In tomato cultivation, the use of AMF has been increased, and their response on yield, biomass production, nutrient uptake [13–16], fruit quality, and improved water relations [17–19] has been documented. For these reasons, the use of these fungi to increase yields in protected systems is suggested [20]. Preite et al. [21] raises the importance of rational water use in intensive tomato production technologies. Similarly, adequate water supply is essential to achieve high tomato yields in greenhouses, where the main source of water supply is irrigation [13].

Currently, there is a market for AMF-based products, which have been used in different crops of agricultural interest. However, some studies suggest that commercial AMF inocula are not always efficient in crops where they are used [22]. It has been stated that soil and climatic conditions determine the relationship between AMF and the host plant [23], which can generate structural and functional differences within the same AMF species, as well as between morphotypes of the same species.

Previous research indicates the effectiveness of the plant–AMF relationship can vary due to the origin of the AMF and the way it is inoculated. Not only does AMF native from semi-arid environments provide high drought resistance by incorporating water and nutrients more efficiently in dry soils, but also the use of mixed inocula containing three or more AMF species may give better results on the host plant than inoculating monospecific AMF [23]. In contrast, better replication in inoculum production can be achieved when using monospecific spores compared to inoculation with mycorrhizal consortia [6]. On the other hand, the high diversity of AMF species existing in tropical environments due to the diversity of plants present in these conditions represents the high potential for use [24]; however, the benefits provided by mycorrhizal fungal communities inhabiting these environments have been the least investigated [25]. Inoculation with monospecific species or AMF consortia may induce a different response in the host plant [26]. Similarly, studies confirm that the type of soil and the host influence the effectiveness of mycorrhizal symbiosis. Some authors have reported differences in the effectiveness of AMF species according to the family to which they belong. For example, high soil nutrient levels affect species of the family Glomeraceae [27,28], however, some species of this family persist under conditions of higher nitrogen supply more than those of the Gigasporaceae family; in terms of germination and host colonization, species of the Claroideoglomeraceae family tend to be more competitive [29], and under acid pH and low-temperature conditions, species of the Acaulosporaceae family develop better [30].

Recent studies have focused on the fruit quality of mycorrhizal tomato plants subjected to water and salt stress conditions; others have focused on fertilization, mainly phosphorus, phosphate acquisition capacity, and phosphate utilization efficiency, which determine mycorrhizal dependence [26]. Although the use of AMF in tomato cultivation has been described, there is insufficient information concerning mycorrhizal specificity and the dependence of tomatoes on specific mycorrhizal species or consortia. Therefore, it is necessary to know whether the mycorrhizal efficiency is determined by the AMF species or consortia inoculated when the plant is subjected to different water stresses, which will allow the establishment of colonization strategies with the most efficient AMF in tomato crops.

Considering the above, the aim of this work was to evaluate AMF species isolated from contrasting environments and their response in tomatoes (*Solanum lycopersicum*) subjected to decreasing water regimes. The above, under the hypothesis that inoculation with arbuscular mycorrhizal fungi isolated from soils of different environments, either in consortium or as a single species, contributes to sustaining growth, yield, and fruit quality, but with variations depending on the origin of the AMF.

2. Materials and Methods

2.1. Description of the Experiment and Experimental Conditions

The experiment was carried out for 140 days in a greenhouse of the Agronomy and Veterinary School of the Universidad Autónoma de San Luis Potosí. The model crop was tomato (*Solanum lycopersicum*, cv. Rio Grande); seedlings were obtained in expanded

polyethylene seedbeds with a mixture of peat, vermiculite, and agrolite (60-20-20) for 6 weeks. At the time of transplanting, the seedlings were placed in 11 L black polyethylene bags (37 cm × 37 cm) with tezontle gravel as substrate. AMF were inoculated into the seedlings seven days after transplanting.

A factorial experiment (4 × 3) was carried out in a completely randomized design with nine replicates for each treatment. The first factor corresponded to four types of AMF inoculums from humid and semi-arid ecosystems, which were applied as single species or in consortium (Table 1). For the selection of the species to be inoculated, either singly or in consortium, they were previously isolated by the ‘wet sieving and decantation’ method [31] and the abundance was determined by the ‘Shannon–Weaver’ method [32]. The species selected were those with the highest abundance.

Table 1. Species used for the assay according to type of inoculation and ecosystem of origin.

Source Ecosystem	Type of Inoculum	
	Monospecific Inoculum (EH and ES)	Inoculum in Consortium (CH and CS)
Humid ecosystem	<i>Glomus</i> sp. 1	<i>Claroideoglomus etunicatum</i> (W.N. Becker and Gerd.) C. Walker and A. Schüssler <i>Funnelformis mosseae</i> (T.H. Nicolson and Gerd.) C. Walker and A. Schüssler <i>Glomus</i> sp. 1 <i>Glomus rubiforme</i> (Gerd. and Trappe) R.T. Almeida and N.C. Schenck
Semi-arid ecosystem	<i>Claroideoglomus etunicatum</i>	<i>Acaulospora morrowiae</i> Spain and N.C. Schenck <i>Claroideoglomus etunicatum</i> <i>Glomus macrocarpum</i> Tul. and C. Tul.

Glomus sp. 1 monospecific inoculum (EH); humid ecosystem consortium (CH); *C. etunicatum* monospecific inoculum (ES); semi-arid ecosystem consortium (CS).

AMF were replicated from spores isolated from soils of two different edaphoclimatic environments, named for this research as a humid ecosystem and a semi-arid ecosystem. In the humid ecosystem, the soil is a luvisol [33] and the climate is semi-warm and humid with year-round rainfall [34]; the predominant plant species according to [35] are *Carya palmeri*, *Chaetoptelea mexicana*, *Clethra pringlei*, *Dalbergia* sp., *Juglans mollis*, *Magnolia dealbata*, *Morus celtidifolia*, *Persea* spp., *Platymiscium* sp., and *Tilia mexicana*, and is a mountain mesophyll forest biome. The site is located in the municipality of Xilitla, San Luis Potosí, Mexico, at the following geographical coordinates: 21°23' N and 98°59' W and at an altitude of 600 to 900 masl. Moreover, in the semi-arid ecosystem, the soil is a leptosol [33] and the climate is dry or arid with summer rainfall regimes [34]; the predominant plant species according to [35] are *Opuntia streptacantha*, *Myrtillocactus geometrizans*, *Prosopis laevigata*, *Mimosa* sp., *Lycium* sp., *Jatropha* sp., and *Agave* sp. and it is a biome called xerophytic scrub. The site is located in the municipality of Villa Hidalgo, San Luis Potosí, Mexico, at the following geographic coordinates: 22°27' N and 100°42' W and at an altitude of 1700 masl.

The second factor was the irrigation doses applied to the plants (100%, 85%, and 70%), which were determined using the “container capacity” method. The method entails saturating a mass of substrate with water and allowing it to drain completely until it reaches a state of equilibrium [36]. The plants were irrigated three times per day, and the volume of irrigation is shown in Table 2. Fertilization was carried out using nutrient solutions according to the phenological stage of the plant [37].

Table 2. Amount of water applied at each irrigation dose.

Irrigation Dose	Water Volume (mL/Day)
100%	830.2 ± 53
85%	706 ± 45.1
70%	581.8 ± 37.2

2.2. Estimation of Mycorrhizal Variables

The mycorrhizal variables under investigation were the percentage and intensity of colonization at the conclusion of the experiment. The former quantifies the presence of mycorrhizal structures within the root, while the latter measures the quantity of mycorrhizal structures present within the root. Roots from the nine replicates per treatment were homogenized and divided into five composite samples for the assessment of the percentage and intensity of colonization. For the study of the percentage and intensity of colonization, thin roots were taken and stained using the method proposed by Phillips and Hayman [38]. The reading was performed by placing 10 fragments of fine roots of about 1 cm in length on a slide, and the structures present in 10 intercepts per root fragment were counted. Mycorrhizal roots were considered as mycorrhizal roots if they contained any mycorrhizal structure (intraradical hyphae, arbuscules, and vesicles) at the intersection points where the reading was made. The reading was performed under a microscope (Nikon Model Eclipse. Japan); the percentage and intensity of colonization were quantified according to Equations (1) and (2) [39].

$$\text{Colonization rate} = \sum B / \sum Z \times 100 \quad (1)$$

$$\text{Intensity of colonization} = \sum A / \sum Z \quad (2)$$

where:

$\sum B$: total number of roots with mycorrhizal structures;

$\sum Z$: total of 100 roots evaluated;

$\sum A$: result of multiplying the mycorrhizal roots observed at each assessment level by a constant set for each level.

Assessment level	0	1	2	3	4	5
Constant set for each level	0	1	2.5	15.5	35.5	47.5

2.3. Evaluation of Fruit Quality

As fruit quality parameters, the equatorial and polar diameters of 10 fruits per treatment were measured using a digital caliper [40], and the total soluble solids content (TSS) °Brix was determined with a digital refractometer HI 96,801 (Hanna Instruments, Smithfield, RI, USA).

2.4. Evaluation of Growth, Development, and Yield

At 119 days after transplanting, when the plants stopped growing, plant height and stem diameter were recorded using a flexometer and a digital caliper. Aerial dry biomass, root dry biomass, and yield (weight and quantity) of fruits were also recorded with a digital technical balance, OHAUS® (Parsippany, NJ, USA). The aerial and root dry biomass samples were dried in a RIOSSA NOM (Rios Rocha, S.A., Mexico City, Mexico) oven at 70 °C to constant weight.

2.5. Statistical Analysis

Data were analyzed by analysis of variance (ANOVA) using Tukey's test ($\alpha = 0.05$) for the multiple comparison of the means. Variables with binomial distribution (percentage and intensity of colonization) were transformed with the function $\arccos \sqrt{\frac{x}{100}}$, while variables with Poisson distribution (number of fruits/plant) were transformed with $\log x$. In addition, each independent inoculum of AMF was analyzed as a function of the three

irrigation doses, using a test for the multiple comparison of the means. All statistical analyses were performed using Minitab15 for Windows v12.0.0.58849.

3. Results

3.1. Mycorrhizal Variables

The percentage and intensity of colonization showed different patterns in relation to the three irrigation doses evaluated (70%, 85%, and 100%) and as a function of AMF origin and inoculation form (Table 3).

Table 3. Analysis of variance results of the simple effects and the interaction of the studied factors on the indicators of mycorrhizal functioning of the tomato plants inoculated with different AMF and subjected to different irrigation doses.

Sources of Variation	ANOVA	
	Colonization (%)	Intensity of Colonization (%)
AMF inoculums	0.001 ***	0.142 ns
Dose of irrigation	0.313 ns	0.099 ns
Interaction	0.001 ***	0.001 ***
SE	1.60	0.15

Standard error (SE). *** $p < 0.001$. ns (Not significant).

The monospecific inoculum (EH) showed the highest values of percentage (43%) and intensity (2.6%) of colonization with the intermediate irrigation dose (85%), while the values were significantly lower with the 70% and 100% irrigation doses. The CH consortium maintained similar colonization percentage values with the 70% and 85% irrigation doses but decreased by 27% with the 100% irrigation dose. Likewise, the intensity of colonization increased with the same irrigation doses, and its values were 54% higher than those observed with the 100% irrigation dose. However, with increasing substrate humidity, the CH consortium decreased the presence of mycorrhizal structures. On the other hand, inoculation with the monospecific inoculum (ES) showed the lowest values of colonization percentage (35%) and intensity (1.2%) with the intermediate irrigation dose (85%), while with the 70% and 100% irrigation doses, the values were significantly higher, with colonization percentages of 43% and 56%, respectively, and intensities of 3.4% and 3.9%, respectively. The species from the semi-arid ecosystem showed the opposite behavior to the monospecific inoculum (EH) in relation to the irrigation doses applied. While the monospecific inoculum (ES) decreased the number of colonized roots and intraradical mycorrhizal structures with the average irrigation dose (85%), the monospecific inoculum (EH) increased them. In the inoculation with CS, the percentage of colonization decreased linearly with increasing irrigation dose; the highest value (51%) was with the 70% irrigation dose, and the lowest (44%) was with the 100% dose. The intensity of colonization was highest at the 70% irrigation dose (2.6) and lowest (1.9%) at the 85% irrigation dose (Figure 1a,b). The CS consortium revealed a similar response to the monospecific inoculum (ES) when the irrigation dose was reduced by 70%, increasing the presence of colonized roots and intraradical mycorrhizal structures. However, its response was different when the higher irrigation dose (100%) was used, even though both inocula have the same ecosystem of origin.

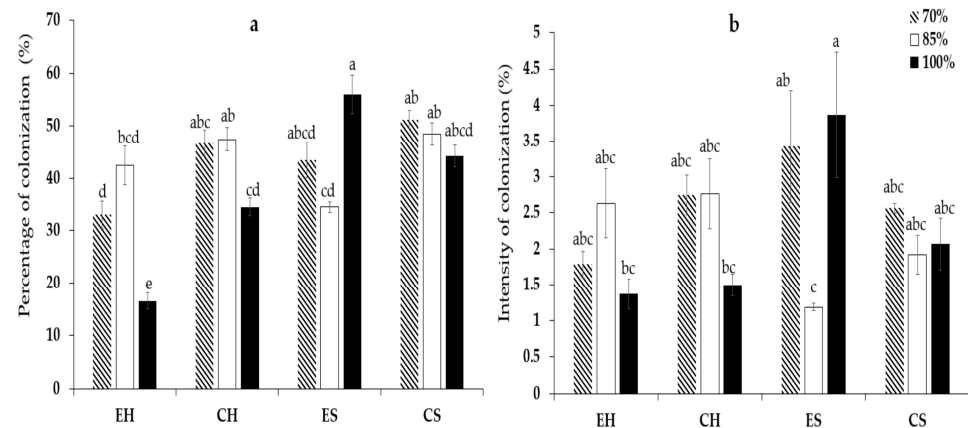


Figure 1. Effect of the inoculum source and the irrigation dose on the mycorrhizal behavior in tomato roots. (a) Percentage of colonization; (b) Intensity of colonization. Bars indicate the mean ($\pm$ standard error). Inoculum sources: *Glomus* sp.1 monospecific inoculum (EH); humid ecosystem consortium (CH); *C. etunicatum* monospecific inoculum (ES); semi-arid ecosystem consortium (CS); irrigation dose: 70%, 85%, and 100%. The same letter indicates did not show a significant difference according to Tukey's test, $\alpha = 0.05$, number of samples is five.

3.2. Fruit Quality

Significant differences were observed in equatorial and polar diameters and TSS in relation to the three irrigation doses evaluated (70%, 85%, and 100%) and as a function of AMF origin and inoculation method (Table 4).

Table 4. Analysis of variance results of the simple effects and the interaction of the studied factors on the fruit quality variables of the tomato plants inoculated with different AMF and subjected to different irrigation doses.

Sources of Variation	ANOVA		
	Equatorial Diameter (mm)	Polar Diameter (mm)	TSS ($^{\circ}$ Bx)
AMF inoculums	0.001 ***	0.001 ***	0.117 ns
Dose of irrigation	0.001 ***	0.001 ***	0.001 ***
Interaction	0.001 ***	0.001 **	0.004 ***
SE	0.23	0.46	0.10

Standard error (SE). Multiple comparison of means according to Tukey's test for ** $p < 0.01$; and *** $p < 0.001$. ns (Not significant)

The results showed that the largest equatorial and polar diameters in fruit were obtained with the monospecific inoculum (ES) when 100% of the irrigation dose was applied (Figure 2). Inocula from the humid ecosystem maintained similar equatorial diameters with the 85% and 100% irrigation doses, while inocula from the semi-arid ecosystem were similar with the 70% and 85% irrigation doses (Figure 2a). With respect to polar diameter, inocula from the humid ecosystem showed no differences at the three irrigation doses, while for the CS consortium, they were similar at the 85% and 100% irrigation doses (Figure 2b).

Regarding TSS, inoculation with monospecific inoculum (EH) at the 70% dose promoted 5.8 $^{\circ}$ Brix higher by 11.4% and 22.6% than those obtained with the 85% and 100% irrigation doses, respectively. The CH consortium showed similar TSS values at the 85% and 100% irrigation doses, which averaged 4.8 $^{\circ}$ Brix and were 27% lower than at the 70% irrigation dose. Monospecific inoculum (ES) inoculation with the 70% dose promoted 6.33 $^{\circ}$ Brix and was 15% and 40% higher than with the 85% and 100% irrigation doses, respectively. In comparison, the CS consortium promoted 5.88 $^{\circ}$ Brix and was 14% and 28% higher than with the 85% and 100% doses, respectively (Figure 3).

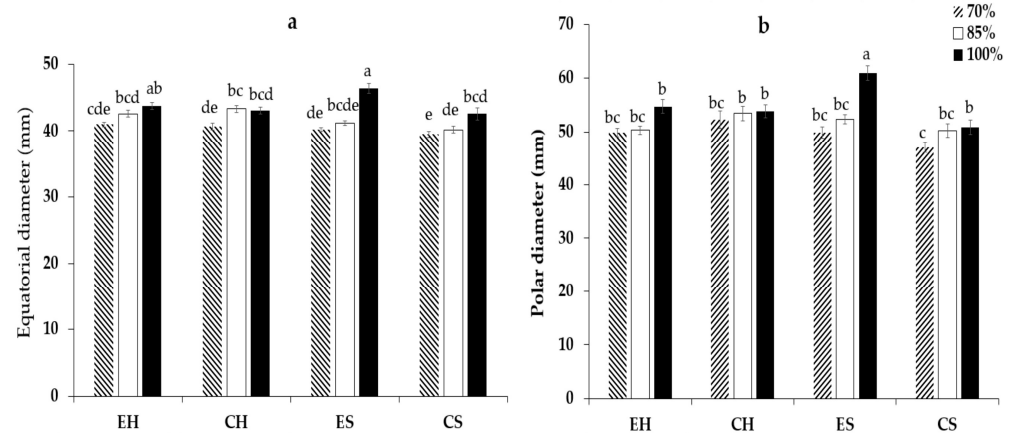


Figure 2. Effect of the inoculum source and the irrigation dose on the quality of the fruit of tomato plants inoculated with mycorrhizal spores. (a) Equatorial diameter; (b) Polar diameter. Bars indicate the mean ($\pm$ standard error). Inoculum sources: *Glomus* sp.1 monospecific inoculum (EH); humid ecosystem consortium (CH); *C. etunicatum* monospecific inoculum (ES); semi-arid ecosystem consortium (CS); irrigation dose: 70%, 85%, and 100%. The same letter indicates did not show a significant difference according to Tukey's test, $\alpha = 0.05$, number of samples is ten.

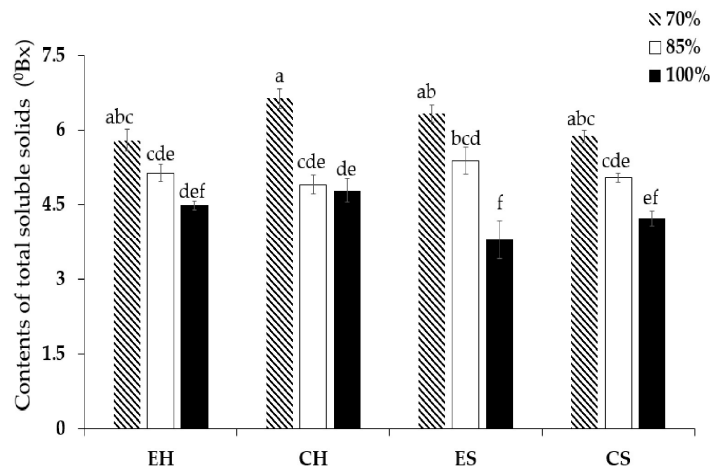


Figure 3. Effect of the inoculum source and the irrigation dose over the contents of total soluble solids in tomato plants inoculated with mycorrhizal spores. Bars indicate the mean ($\pm$ standard error). Inoculum sources: *Glomus* sp.1 monospecific inoculum (EH); humid ecosystem consortium (CH); *C. etunicatum* monospecific inoculum (ES); semi-arid ecosystem consortium (CS); irrigation dose: 70%, 85%, and 100%. The same letter indicates did not show a significant difference according to Tukey's test, $\alpha = 0.05$, number of samples is ten.

3.3. Growth and Yield

The application of AMF inoculum sources (monospecific or consortium) from a humid ecosystem resulted in a reduction in plant height when compared to AMF inocula from a semi-arid ecosystem. The latter promoted height values of 69 cm, a 5% increase over those obtained with the monospecific inoculum (EH) and consortium (CH). This indicates that these species demonstrated the greatest adaptation to the established irrigation doses, particularly the 85% and 70% irrigation doses (Tables 5 and 6).

Table 5. Analysis of variance results of the simple effects and the interaction of the studied factors on the growth and yield variables of the tomato plants inoculated with different AMF and subjected to different irrigation doses.

Sources of Variation	ANOVA			
	Plant Height (cm)	Stem Diameter (mm)	Yield (g/Plant)	Quantity (Fruits/Plant)
AMF inoculums	0.009 **	0.593 ns	0.822 ns	0.892 ns
Dose of irrigation	0.500 ns	0.001 ***	0.001 ***	0.001 ***
Interaction	0.985 ns	0.547 ns	0.453 ns	0.201 ns
SE	0.23	0.01	46.9	0.87

Standard error of measurement (SE). ** $p < 0.01$; and *** $p < 0.001$. ns (Not significant).

Table 6. Results of the independent factors in the growth and yield variables of tomato plants inoculated with different AMF and subjected to different doses of irrigation.

Independent Factors	ANOVA			
	Plant Height (cm)	Stem Diameter (mm)	Yield (g/Plant)	Quantity (Fruits/Plant)
AMF Inoculums				
EH	65.2 b	1.73	2213.4	64.8
CH	65.3 b	1.74	2228.6	64.5
ES	68.9 a	1.75	2243.7	63.44
CS	69.2 a	1.71	2193.3	63.44
Dose of irrigation				
70%	66.3	1.67 b	1730.6 c	61.2 c
85%	67.6	1.74 a	2220.9 b	63.4 b
100%	67.7	1.79 a	2707.7 a	67.6 a

Glomus sp.1 monospecific inoculum (EH); humid ecosystem consortium (CH); *C. etunicatum* monospecific inoculum (ES); semi-arid ecosystem consortium (CS). The value followed by the same letter in the same column did not show a significant difference according to Tukey's test, $\alpha = 0.05$; number of samples is nine.

Stem diameter was dependent on irrigation dose; 100% and 85% irrigation doses averaged significantly larger stems (1.8 cm), higher by 5% than in plants with 70% irrigation doses (Tables 5 and 6). This suggests that up to 15% less irrigation can be used in plants, and water use efficiency is achieved, promoting similar stem size per unit of water transpired.

4. Discussion

4.1. Mycorrhizal Variables

The results suggest that the AMF species respond in different ways when the water supply is reduced. The monospecific inocula (EH and ES) did not respond similarly, which may be due to the ecosystem of origin or the manner in which these species were applied. It is important to note that both species were part of a native consortium and were inoculated in isolation due to their high ability to adapt and replicate. This indicates that both AMF species show different mechanisms of adaptation to water deficit. On the other hand, it was observed that the percentage and intensity of colonization decreased in the consortia as the irrigation dose increased. Although both had similar behavior, the pattern of their responses depended on the ecosystem of origin. One possible explanation for the response found in the consortia may be due to the synergism present between the species that make up the consortia and the contribution that each of them makes to the symbiosis. Among the mechanisms involved in the mycorrhizal symbiosis that influence the efficiency of AMF is the morpho-anatomical transformation of the root system due to the increase in extraradical mycelium, which favors the increase of hyphae, arbuscules, and vesicles inside the root. An increase in these mycorrhizal structures inside and outside the root may serve as an indicator that the functional differences observed among certain AMF groups are dependent on edaphic and host crop conditions.

The abundance of arbuscular mycorrhizal structures on host roots is related to the abundance of AMF species in the soil [41]. Similarly, in colonization with individual mycorrhizal species, the increase of mycorrhizal structures on the root can be compensated by different colonization strategies [8]. For example, there are AMF species that are very efficient in developing abundant mycorrhizal structures under water stress conditions [42]. Consequently, an increase in root colonization will depend on the AMF species and the increase in extraradical mycelium [29]. *Claroideoglomus etunicatum* is a species of AMF that exhibits high levels of mycorrhizal colonization [43], and the results obtained in this experiment demonstrated the efficiency of this mycorrhizal species. Furthermore, it is important to highlight that, within the rhizospheric microbial community, including AMF, synergistic interactions exist that contribute to the enhancement of mycorrhizal structures within the root system. Additionally, this may be associated with an increase in the diversity of AMF species [8].

The results confirm that each mycorrhizal structure has distinctive characteristics and reveal structure-specific expression patterns of genes related to nutrient transport and metabolism of branched absorbing structures (BASs). The biochemistry of BASs in mycorrhizal symbiosis nutrition has been documented; for example, expression of genes encoding glutamine synthase is highest in germ tubes; genes encoding nitrate and urea transporters are highly expressed in the runner hyphae and are suppressed in germ tubes; genes related to arginine metabolism are expressed among extraradical structures, but with a particular pattern; while genes encoding aquaporin, *AQP1*, are specifically expressed in immature spores [44].

4.2. Fruit Quality

The inoculation of AMF species from a humid environment did not affect fruit size when substrate moisture was reduced by 15%. These AMF species demonstrated superior adaptation, as evidenced by the high prevalence of mycorrhizal structures within the roots when the irrigation dose was 85%. The mycorrhizal symbiosis contributes to the improvement of the quality of the fruits, which are the most important nutrient sinks [45]. Mycorrhizal plants can increase the uptake of phosphorus, copper, and zinc [17]; significant increases in fruit length, diameter, and weight were documented by Carrillo et al. [46]. Our results showed similar fruit sizes of monospecific inoculum (EH) inoculated plants under the three irrigation doses, and this response may be due to efficient nutrient uptake. On the other hand, inoculation with monospecific inoculum (ES) decreased fruit size when the water supply was reduced, even though this species was isolated from a semi-arid environment. From the monospecific inoculum (ES), we expected a greater tolerance to water deficit due to the high levels of root colonization with the 70% irrigation dose; however, although it promoted greater fruit size, this was due to the 100% irrigation dose. This leads us to consider whether the efficacy of the monospecific inoculum (ES) under water deficit will be subject to it being part of an AMF consortium.

The results show that the increase in TSS was not due to inoculation with the different AMF types and suggest that it was due to the decrease in substrate moisture. The different types of mycorrhizal inocula successfully colonized the roots of tomato plants and increased water uptake. In contrast, fruit soluble solids content decreased when the plants were well irrigated. The effects of AMF may also be due to the fact that AMF species differ in their efficiency of enhancing the uptake of water and nutrients to the plant from the soil [47]. Candido et al. [14] and Bakr et al. [16] reported increases in TSS associated with water stress rather than AMF colonization, a finding that is consistent with the results of the present study. While AMF species did not have an effect on TSS, it is important to note that an increase in TSS has a positive influence on the reduction of fruit processing costs [48].

4.3. Growth and Yield

The observed water use efficiency in diameter growth possibly reflects physiological mechanisms as reported by Yang et al. [49] and Du et al. [50]. As for the interaction of

the factors under study, it was not significant on any of the growth variables. Reducing irrigation could improve the efficiency of water use by plants [49]; these authors compared lower irrigation doses with full irrigation, and their results reflected slight decreases in plant growth and yield. The importance of osmotic adjustment and chemical growth regulators in roots should be taken into account, as they maintain the water status of plants, and their reduction would have an impact on plant growth [4]. The increase in plant height is consistent with a greater presence of mycorrhizal structures in the roots where AMF from a semi-arid ecosystem was applied. The increase in plant height can be attributed to an increase in nutrient and water uptake. It has been documented that species from stressed environments develop adaptive mechanisms, such as increased BASs, which allow greater water and nutrient uptake in case of water deficit.

Sagadin et al. [23] reports that AMF from semi-arid environments show a higher proliferation of extraradical mycelium. The variations that occur in hormone balance (ABA, strigolactones, and jasmonic acid) are another fundamental mechanism in the development and functionality of the structures responsible for the transport of nutrients and water to the plant; these changes in hormone levels may depend on the AMF species and the host plant [51]. On the other hand, in mycorrhizal symbioses, the relationship between plant growth and metabolism will depend on the efficiency with which the AMF species utilizes the carbon fixed by the plant [45,46]. Ryan and Graham [22] suggest that the genotype of the host plant, that of the AMF, and the interaction of the two ensure higher growth and quality of their host.

The changes in yield and fruit quantity were due to the amount of water applied and not to the type of inoculum or the way it was applied (Table 6). Water accounts for 95% of the total weight of the tomato fruit, making it an essential component. Given that tomatoes are very sensitive to water stress during their different phenological phases, from germination to fruit set [52], adequate irrigation is recommended according to the physiological needs of the crop. However, since some reductions in irrigation did not demerit some quality traits of the fruit, from a commercial and benefits point of view, it might be recommended to evaluate how suitable a reduction in yield could be, knowing that maintenance of quality can maintain income.

5. Conclusions

Colonization with monospecific inocula (EH and ES) showed contrasting differences at 85% and 100% irrigation rates. With gradually increasing irrigation rates, colonization decreased with the CH consortium, while the CS consortium showed similar colonization levels at all three irrigation rates. AMF from humid environments (monospecific or in the consortium) did not affect equatorial diameter when the irrigation rate was reduced by 15%, while polar diameter was similar at all three irrigation rates. Inocula from the semi-arid ecosystem promoted the greatest equatorial and polar diameters at the 100% irrigation dose. The monospecific inoculum of *C. etunicatum* (ES) showed great potential to promote plant growth and development at the 100% irrigation dose and could be a biotechnological tool to improve tomato yield under conditions similar to those of this study.

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References

- Walder, F.; van der Heijden, M.G.A. Regulation of Resource Exchange in the Arbuscular Mycorrhizal Symbiosis. *Nat. Plants* **2015**, *1*, 15159. [\[CrossRef\]](#) [\[PubMed\]](#)
- Bahadur, A.; Batool, A.; Nasir, F.; Jiang, S.; Mingsen, Q.; Zhang, Q.; Pan, J.; Liu, Y.; Feng, H. Mechanistic Insights into Arbuscular Mycorrhizal Fungi-Mediated Drought Stress Tolerance in Plants. *Int. J. Mol. Sci.* **2019**, *20*, 4199. [\[CrossRef\]](#) [\[PubMed\]](#)
- Thangavel, P.; Anjum, N.A.; Muthukumar, T.; Sridevi, G.; Vasudhevan, P.; Maruthupandian, A. Arbuscular Mycorrhizae: Natural Modulators of Plant-Nutrient Relation and Growth in Stressful Environments. *Arch. Microbiol.* **2022**, *204*, 264. [\[CrossRef\]](#)
- Mitra, D.; Djebaili, R.; Pellegrini, M.; Mahakur, B.; Sarker, A.; Chaudhary, P.; Khoshru, B.; Del Gallo, M.; Mahmoud, K.; Barik, D.; et al. Arbuscular Mycorrhizal Symbiosis: Plant Growth Improvement and Induction of Resistance under Stressful Conditions. *J. Plant Nutr.* **2021**, *44*, 1993–2028. [\[CrossRef\]](#)
- Mathur, S.; Tomar, R.; Jajoo, A. Arbuscular Mycorrhizal Fungi (AMF) Protects Photosynthetic Apparatus of Wheat under Drought Stress. *Photosynth. Res.* **2019**, *139*, 227–238. [\[CrossRef\]](#) [\[PubMed\]](#)
- Berruti, A.; Lumini, E.; Balestrini, R.; Bianciotto, V. Arbuscular Mycorrhizal Fungi as Natural Biofertilizers: Let's Benefit from Past Successes. *Front. Microbiol.* **2016**, *6*, 1559. [\[CrossRef\]](#)
- Wu, S.; Shi, Z.; Chen, X.; Gao, J.; Wang, X. Arbuscular Mycorrhizal Fungi Increase Crop Yields by Improving Biomass under Rainfed Condition: A Meta-Analysis. *PeerJ* **2022**, *10*, e12861. [\[CrossRef\]](#)
- Smith, F.A.; Smith, S.E. How Harmonious Are Arbuscular Mycorrhizal Symbioses? Inconsistent Concepts Reflect Different Mindsets as Well as Results. *New Phytol.* **2015**, *205*, 1381–1384. [\[CrossRef\]](#)
- Dey, M.; Ghosh, S. Arbuscular Mycorrhizae in Plant Immunity and Crop Pathogen Control. *Rhizosphere* **2022**, *22*, 100524. [\[CrossRef\]](#)
- Chen, M.; Arato, M.; Borghi, L.; Nouri, E.; Reinhardt, D. Beneficial Services of Arbuscular Mycorrhizal Fungi—From Ecology to Application. *Front. Plant Sci.* **2018**, *9*, 1270. [\[CrossRef\]](#)
- FAO, UN Water. *Progress on the Level of Water Stress: Global Status and Acceleration Needs for SDG Indicator 6.4.2*; FAO, United Nations Water (UN Water): Rome, Italy, 2021; 95p.
- Bennett, A.E.; Classen, A.T. Climate change influences mycorrhizal fungal–plant interactions, but conclusions are limited by geographical study bias. *Ecology* **2020**, *101*, e02978. [\[CrossRef\]](#) [\[PubMed\]](#)
- Biel, C.; Camprubi, A.; Lovato, P.E.; Calvet, C. On-Farm Reduced Irrigation and Fertilizer Doses, and Arbuscular Mycorrhizal Fungal Inoculation Improve Water Productivity in Tomato Production. *Sci. Hortic.* **2021**, *288*, 110337. [\[CrossRef\]](#)
- Candido, V.; Campanelli, G.; D'Addabbo, T.; Castronuovo, D.; Perniola, M.; Camele, I. Growth and Yield Promoting Effect of Artificial Mycorrhization on Field Tomato at Different Irrigation Regimes. *Sci. Hortic.* **2015**, *187*, 35–43. [\[CrossRef\]](#)
- Michałojć, Z.; Jarosz, Z.; Pitura, K.; Dzida, K. Effect of Mycorrhizal Colonization and Nutrient Solutions Concentration on the Yielding and Chemical Composition of Tomato Grown in Rockwool and Straw Medium. *Acta Sci. Pol. Hortorum Cultus* **2015**, *14*, 15–27.
- Bakr, J.; Daood, H.; Pék, Z.; Helyes, L.; Posta, K. Yield and Quality of Mycorrhized Processing Tomato under Water Scarcity. *Appl. Ecol. Environ. Res.* **2017**, *15*, 401–413. [\[CrossRef\]](#)
- Wahb-Allah, M.A.; Abdel-Razzak, H.S.; Alsadon, A.A.; Ibrahim, A.A. Growth, Yield, Fruit Quality and Water Use Efficiency of Tomato under Arbuscular Mycorrhizal Inoculation and Irrigation Level Treatments. *Life Sci. J.* **2014**, *11*, 109–117.
- Chitarra, W.; Pagliarini, C.; Maserti, B.; Lumini, E.; Siciliano, I.; Cascone, P.; Schubert, A.; Gambino, G.; Balestrini, R.; Guerrieri, E. Insights On the Impact of Arbuscular Mycorrhizal Symbiosis On Tomato Tolerance to Water Stress. *Plant Physiol.* **2016**, *171*, 1009–1023. [\[CrossRef\]](#)
- Volpe, V.; Chitarra, W.; Cascone, P.; Volpe, M.G.; Bartolini, P.; Moneti, G.; Pieraccini, G.; Di Serio, C.; Maserti, B.; Guerrieri, E.; et al. The Association With Two Different Arbuscular Mycorrhizal Fungi Differently Affects Water Stress Tolerance in Tomato. *Front. Plant Sci.* **2018**, *9*, 1480. [\[CrossRef\]](#) [\[PubMed\]](#)
- Morales-Guevara, D.; Rodríguez-Larramendi, L.; Dell'Amico-Rodríguez, J.; Jerez-Mompie, E.; Estrada-Prado, W. Efecto de dos bioestimulantes y hongos micorrízico en plantas de tomate sembradas a altas temperaturas. *Cult. Trop.* **2018**, *39*, 41–48.
- Preite, L.; Solari, F.; Vignali, G. Technologies to Optimize the Water Consumption in Agriculture: A Systematic Review. *Sustainability* **2023**, *15*, 5975. [\[CrossRef\]](#)
- Ryan, M.H.; Graham, J.H. Little Evidence That Farmers Should Consider Abundance or Diversity of Arbuscular Mycorrhizal Fungi When Managing Crops. *New Phytol.* **2018**, *220*, 1092–1107. [\[CrossRef\]](#)
- Sagadin, M.B.; Monteoliva, M.I.; Luna, C.M.; Cabello, M.N. Diversity and Infectivity of Native Arbuscular Mycorrhizal Fungi from Prosopis Alba Areas with Contrasting Edaphoclimatic Characteristics in the Argentinian Parque Chaqueño. *AgriScientia* **2018**, *35*, 19–33. [\[CrossRef\]](#)

24. Álvarez-Sánchez, F.; Sánchez-Gallen, I.; Cuevas, L.; Oro, L.; Meli, P. Diversidad, Abundancia y Variación Estacional En La Comunidad de Hongos Micorrizógenos Arbusculares En La Selva Lacandona, Chiapas, México. *Sci. Fungorum* **2017**, *45*, 37–51. [\[CrossRef\]](#)
25. Van der Heijden, M.G.A.; Martin, F.M.; Selosse, M.-A.; Sanders, I.R. Mycorrhizal Ecology and Evolution: The Past, the Present, and the Future. *New Phytol.* **2015**, *205*, 1406–1423. [\[CrossRef\]](#)
26. Ortas, I. *Mycorrhizas in Fruit Nutrition: Important Breakthroughs*; Elsevier: Amsterdam, The Netherlands, 2020; pp. 339–351. [\[CrossRef\]](#)
27. Šmilauer, P.; Šmilauerová, M.; Kotlínek, M.; Košnar, J. Arbuscular Mycorrhizal Fungal Communities of Forbs and C3 Grasses Respond Differently to Cultivation and Elevated Nutrients. *Mycorrhiza* **2021**, *31*, 455–470. [\[CrossRef\]](#)
28. Treseder, K.K.; Allen, E.B.; Egerton-Warburton, L.M.; Hart, M.M.; Klironomos, J.N.; Maherali, H.; Tedersoo, L. Arbuscular mycorrhizal fungi as mediators of ecosystem responses to nitrogen deposition: A trait based predictive framework. *J. Ecol.* **2018**, *106*, 480–489. [\[CrossRef\]](#)
29. Šmilauer, P.; Košnar, J.; Kotlínek, M.; Pecháčková, S.; Šmilauerová, M. Host Age and Surrounding Vegetation Affect the Community and Colonization Rates of Arbuscular Mycorrhizal Fungi in a Temperate Grassland. *New Phytol.* **2021**, *232*, 290–302. [\[CrossRef\]](#)
30. Davison, J.; Moora, M.; Semchenko, M.; Adenan, S.B.; Ahmed, T.; Akhmetzhanova, A.A.; Alatalo, J.M.; Al-Quraishy, S.; Andriyanova, E.; Anslan, S.; et al. Temperature and pH Define the Realised Niche Space of Arbuscular Mycorrhizal Fungi. *New Phytol.* **2021**, *231*, 763–776. [\[CrossRef\]](#)
31. Gerdemann, J.W.; Nicolson, T.H. Spores of Mycorrhizal Endogone Species Extracted from Soil by Wet Sieving and Decanting. *Trans. Br. Mycol. Soc.* **1963**, *46*, 235–244. [\[CrossRef\]](#)
32. Magurran, A.E. *Measuring Biological Diversity*, 1st ed.; Cornwall: Cornwall, UK, 2004.
33. Anjos, L.; Gaistard, C.; Deckers, J.; Dondeyne, S.; Eberhardt, E.; Gerasimova, M.; Harms, B.; Jones, A.; Krasilnikov, P.; Reinsch, T.; et al. *World Reference Base for Soil Resources 2014 International Soil Classification System for Naming Soils and Creating Legends for Soil Maps*; JRC91947; Schad, P., Van Huyssteen, C., Micheli, E., Eds.; FAO: Rome, Italy, 2015.
34. García, E. *Modificaciones al Sistema de Clasificación Climática de Köppen*, 5th ed.; CONABIO: Ciudad de México, Mexico, 2004; 97p.
35. Rzedowski, J. *Vegetation of Mexico*, 1st ed.; Comisión Nacional para el Conocimiento y Uso de la Biodiversidad: Ciudad de México, Mexico, 2006; 504p.
36. Martínez, P.F.; Roca, D. Sustratos Para El Cultivo Sin Suelo. Materiales, Propiedades Y Manejo. In *Sustratos, Manejo Del Clima, Automatización Y Control En Sistemas de Cultivo Sin Suelo*; Victor, J., Flórez, R., Eds.; Editorial Universidad Nacional de Colombia: Bogotá, Colombia, 2011; pp. 37–77.
37. Castellanos Ramos, J.Z. *Manual de Producción de Tomate En Invernadero*; Soluciones Impresas OCMA: Celaya, Mexico, 2009.
38. Phillips, J.M.; Hayman, D.S. Improved Procedures for Clearing Roots and Staining Parasitic and Vesicular-Arbuscular Mycorrhizal Fungi for Rapid Assessment of Infection. *Trans. Br. Mycol. Soc.* **1970**, *55*, 158–IN18. [\[CrossRef\]](#)
39. Trouvelot, A.; Kough, J.L.; Gianinazzi-Pearson, V. Estimation of VA Mycorrhizal Infection Levels. Research for Methods Having a Functional Significance. In *Proceedings of the 1st European Symposium on Mycorrhizae*, Dijon, France, 1–5 July 1985.
40. Casierra-Posada, F.; Cardozo, M.; Julián, F. Cárdenas-Hernández. Análisis del crecimiento en frutos de tomate (*Lycopersicon esculentum* Mill.) cultivados bajo invernadero. *Agron. Colomb.* **2007**, *25*, 299–305.
41. Barceló, M.; van Bodegom, P.M.; Tedersoo, L.; den Haan, N.; Veen, G.F.; Ostonen, I.; Trimbos, K.; Soudzilovskaia, N.A. The Abundance of Arbuscular Mycorrhiza in Soils Is Linked to the Total Length of Roots Colonized at Ecosystem Level. *PLoS ONE* **2020**, *15*, e0237256. [\[CrossRef\]](#)
42. Kumar, A.; Verma, J.P. Does Plant—Microbe Interaction Confer Stress Tolerance in Plants: A Review? *Microbiol. Res.* **2018**, *207*, 41–52. [\[CrossRef\]](#)
43. Jamiolkowska, A.; Thanon, A.H.; Skwarylo, B.; Patkowska, E.; Mielniczuk, E. Mycorrhizal Inoculation as an Alternative for the Ecological Production of Tomato (*Lycopersicon esculentum* Mill.). *Int. Agrophys.* **2020**, *34*, 253–264. [\[CrossRef\]](#)
44. Kameoka, H.; Maeda, T.; Okuma, N.; Kawaguchi, M. Structure-Specific Regulation of Nutrient Transport and Metabolism in Arbuscular Mycorrhizal Fungi. *Plant Cell Physiol.* **2019**, *60*, 2272–2281. [\[CrossRef\]](#)
45. Bowles, T.M.; Jackson, L.E.; Loehrer, M.; Cavagnaro, T.R. Ecological Intensification and Arbuscular Mycorrhizas: A Meta-Analysis of Tillage and Cover Crop Effects. *J. Appl. Ecol.* **2017**, *54*, 1785–1793. [\[CrossRef\]](#)
46. Carrillo, M.; Franco, A.; Río, M. Productividad de Tomate Mediante Micorriza Arbuscular En Agricultura Protegida. *Rev. Mex. Cienc. Agric.* **2018**, *5*, 513–518. [\[CrossRef\]](#)
47. Stock, S.C.; Koester, M.; Boy, J.; Godoy, R.; Nájera, F.; Matus, F.; Merino, C.; Abdallah, K.; Leuschner, C.; Spielvogel, S.; et al. Plant Carbon Investment in Fine Roots and Arbuscular Mycorrhizal Fungi: A Cross-Biome Study on Nutrient Acquisition Strategies. *Sci. Total Environ.* **2021**, *781*, 146748. [\[CrossRef\]](#)
48. Chafai, W.; Haddioui, K.; Caid, H.; Labazi, H.; AlZain, M.; Noman, O.; Parvez, M.; Addi, M.; Khalid, A. Impact of Arbuscular Mycorrhizal Fungal Strains Isolated from Soil on the Growth, Yield, and Fruit Quality of Tomato Plants under Different Fertilization Regimens. *Horticulturae* **2023**, *9*, 973. [\[CrossRef\]](#)
49. Yang, H.; Du, T.; Qiu, R.; Chen, J.; Wang, F.; Li, Y.; Wang, C.; Gao, L.; Kang, S. Improved Water Use Efficiency and Fruit Quality of Greenhouse Crops under Regulated Deficit Irrigation in Northwest China. *Agric. Water Manag.* **2016**, *179*, 193–204. [\[CrossRef\]](#)

50. Du, T.; Kang, S.; Zhang, J.; Davies, W.J. Deficit Irrigation and Sustainable Water-Resource Strategies in Agriculture for China's Food Security. *J. Exp. Bot.* **2015**, *66*, 2253–2269. [[CrossRef](#)] [[PubMed](#)]
51. Nazareno Saparrat, M.C.; Ruscitti, M.F.; Arango, M.C. *Micorrizas Arbusculares: Biología y Aplicaciones En El Sector Agroforestal*, 1st ed.; Editorial de la Universidad Nacional de La Plata (EDULP): Buenos Aires, Argentina, 2020; 135p.
52. Florido, M.; Fundora, L. Tolerancia a estrés por déficit hídrico en tomate (*Solanum lycopersicum* L.). *Cult. Trop.* **2014**, *35*, 70–88.

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