Arbuscular mycorrhizal fungi improve water use, nutrient uptake, and fruit quality in strawberries

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ABSTRACT

Objective: To evaluate the water expenditure of two strawberry cultivars (Albion and San Andreas) inoculated with three arbuscular mycorrhizal fungi (AMF) grown in two substrates. Moreover, to determine their efficiency in the strawberry plant nutrition and fruit quality.

Design/Methodology/Approach: Five treatments were established: plants inoculated with *Funneliformis geosporum*, *F. mosseae* BEG25, and *F. mosseae* Mich; with conventional management (M. conv), and control. Water consumption, photosynthetic pigments, plant macro- and micronutrient concentrations, soluble sugar concentration, titratable acidity, pH, and Brix degrees in fruits, and mycorrhizal colonization and glomalin concentration were analyzed.

Results: In both substrates, the lowest water consumption was observed in plants inoculated with *F. mosseae* Mich. Plants inoculated with *F. mosseae* BEG25 had similar foliar and fruit concentrations of almost all nutrients analyzed to those of plants with the M. conv treatment. Fruits from inoculated plants had higher Brix degrees, total sugars, glucose, and citric acid than these parameters in control plants.

Limitations/Implications of the study: Although inoculated plants received 40% less nutrient solution (with fertilizer cost savings of US$461 per ha), these showed improved plant nutrition and fruit quality.

Findings/Conclusions: AMF inoculation is a promising strategy for strawberry production under greenhouse conditions, with savings in water and fertilizer use.

Keywords: Arbuscular mycorrhiza, moisture retention, climate change.

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INTRODUCTION

Food safety and food sovereignty are among the most important challenges faced by humanity, and aggravated by global climate change, growing demographics, and urbanization (Abbas *et al.*, 2025). Climate change promotes droughts and reduces water availability for agriculture (Sosa-Hernandez *et al.*, 2019). Agriculture consumes approximately 70% of the water withdrawn from aquifers (Mendelsohn, 2016). Low water availability for agricultural production reduces crop yields since water (approximately 80%) is the main component of 90% of fruits and vegetables (Popkin *et al.*, 2010).

Strawberries (*Fragaria×ananassa* Duch) are a high-demand product due to their flavor and nutritional value (Mikiciuk *et al.*, 2019). Strawberries are rich in nutrients, organic acids, phenolic compounds, flavonoids, and anthocyanins (Urün *et al.*, 2021), making them a functional food with high antioxidant activity. According to Giampieri *et al.* (2015), these metabolites help prevent chronic (such as diabetes and hypertension) and degenerative diseases (like cancer). A serious concern is that strawberry cultivation requires large amounts of water and is highly susceptible to drought (Raturi *et al.*, 2023). This vulnerability is intensified in countries with limited water availability (Audefroy, 2015). Low water availability restricts crop development and productivity, leading to unviable open-field production. Therefore, producers will be gradually forced to abandon open-field food production and opt for technologies such as greenhouse conditions, which predominantly use substrates (Gruda *et al.*, 2019).

Greenhouse production offers clear advantages over soil-based production, including an extended growing season, easier harvesting, and reduced soil-borne diseases. Moreover, the main advantage of greenhouse production is that it provides greater control over irrigation regimes, although it may require more water than traditional agriculture (Robinson-Boyer *et al.*, 2016). Therefore, alternatives must be explored to retain moisture in substrates, increase plant water availability, and improve food quality.

Peat moss is a common component of substrate formulations in protected agriculture (Krueger *et al.*, 2018). However, its extensive agricultural use has a negative environmental impact: extracting peat moss from wetlands impedes CO_2 fixation in these areas. This important ecological function regulates the water cycle and climate (Oberpaur *et al.*, 2010); therefore, it is required to find alternative substrate components with a lower environmental impact. Conversely, rice husk, a byproduct generated in large quantities worldwide, does not affect plant growth (Kumar *et al.*, 2013). In Mexico, annual rice production is expected to reach 350 million tons (SAGARPA, 2017). It is estimated that one ton of husk is generated for every four tons of rice, equivalent to approximately 87.5 million tons of this byproduct per year. This material contributes to the circular economy because of its status as an agricultural residue, and is also a more economical option than peat moss. This makes it an affordable alternative for producers that may reduce production costs and environmental impact.

Inoculation with arbuscular mycorrhizal fungi (AMF) is a biotechnological tool in plant production. These microorganisms form one of the most ubiquitous symbioses in the ground plant community (Smith and Read, 2010; Kuyper and Jansa, 2023). AMF hyphae function as an extended root system that increases the surface area and soil exploration volume, increasing nutrient uptake (Finlay, 2008; Begum *et al.*, 2019). Moreover, AMF modify the extension of the root system, impacting soil structure (Daynes *et al.*, 2013) by forming aggregates and thereby enhancing water retention (Augé *et al.*, 2001; Akter *et al.*, 2024). This suggests that inoculating crops with AMF could lead to more efficient water use. The effect of AMF on strawberry production has been widely recognized (Chávez and Ferrera-Cerrato, 1990; Bona *et al.*, 2015), but their role in substrate moisture retention has been poorly studied. Therefore, this study aimed: 1) To evaluate the water expenditure of two strawberry cultivars

(Albion and San Andreas) inoculated with arbuscular mycorrhizal fungi (AMF) in two growth substrates, and 2) To determine the efficiency of three AMF in the nutrition of strawberry plants and their fruit quality. The hypotheses according to objectives were: 1) Inoculation of strawberry plants with at least one of the AMF decreases water expenditure in strawberry plants, 2) Strawberry plants inoculated with at least one of the AMF increase their fruit quality.

MATERIALS AND METHODS

Experimental design and setup

Two experiments were established to determine the effect of AMF inoculation on water consumption. The first experiment used substrate 1, with the following composition: 50% vermiculite, 25% peat moss, and 25% coconut fiber. The second experiment used substrate 2, consisting of 50% vermiculite, 25% rice husk, and 25% coconut fiber. The first experiment was conducted from March to August 2023, while the second experiment was conducted from July to December 2023. Both experiments were conducted in the same greenhouse, but climatic conditions varied. Therefore, comparisons between the results of the two substrates were not possible, and the results are presented separately for the two substrates tested.

The experiments were established under a completely randomized design. For each experiment, we used two strawberry cultivars: Albion and San Andreas. Each of these cultivars was either 1) inoculated with *Funneliformis geosporum*, 2) inoculated with *Funneliformis mosseae* Mich, 3) inoculated with *Funneliformis mosseae* (BEG25), 4) grown under conventional management (M. conv), or 5) grown as a control treatment (without fungal inoculation). Each treatment was replicated five times, resulting in 50 experimental units for each experiment. In both experiments, all treatments were irrigated twice a week with tap water and once with Hoagland nutrient solution during the growth stage and until flowering, except M. conv, which was irrigated with Hoagland solution twice a week and once with tap water. Similarly, in both experiments, all treatments were irrigated as the M. conv during the early flowering stage until harvest. For inoculated treatments, the nutrient solution was a modified Hoagland solution (Miller and Kitt, 1992), low in phosphorus (20 μM KH_2PO_4) to prevent inhibition of AMF establishment (root colonization) and fungal functionality. The M. conv treatment involved a complete Hogland solution for nutrient management in strawberry plants to mimic conventional management and contrast the potencial plant growth and nutritional benefits of AMF, even when using a nutrient solution with lower phosphorus concentrations. Under this management perspective, the results will compare treatments independently of differences in the nutrient solution tested.

Field capacity (FC, water retained at 30.4 kPa) and permanent wilting point (PWP, water retained at 1,519.9 kPa) were determined for both substrates in the pressure pot and pressure membrane, respectively (Richards, 1956). Bulk density (ρ_b) with the test tube method. With the FC, PWP, and ρ_b data, readily available water (RAW) was calculated with the following equation:

$$RAW = \frac{FC - PWP}{100} \times Z \times \rho_b \times 0.2$$

where: *RAW* is readily available water, *FC* is field capacity (%), *PWP* is the permanent wilting point (%), *Z* is the depth of the substrate in the pot (cm), ρ_b is bulk density (g cm^{-3}), and 0.2 is the depletion factor for strawberries.

Equation 1 determined the volume necessary to have 100% RAW. To quantify the water expenditure of the strawberries in both substrates, we determined substrate moisture using a moisture meter (Lincoln, model 6400/6405). When the % of RAW decreased, water or nutrient solution was added to reach 100% RAW. These adjustments were performed every third day for each experimental unit in both experiments.

Nutrient concentration in leaves and fruits

In both experiments, the concentration of nutrients in the leaf (middle leaves) and fruit was determined by wet digestion of the tissue, according to Jones and Case (1990). The plant material (0.5 g) was weighed and placed in digestion tubes added with 1 mL of 30% hydrogen peroxide and 4 mL of the acid mixture of H_2SO_4-$HClO_4$ (4:1 ratio). Then, the tubes were placed in the digestion oven at 240 °C until the samples became transparent. Finally, the samples were made to 25 mL and filtered with Whatman No. 42 paper. N was quantified in the digestion solution by the Microkjeldahl method, as described by Isaac and Johnson (1976). P concentration was quantified following Murphy and Riley's method (1962) with a Varian UV-visible spectrophotometer (Cary 50). K concentration was measured by flammetry (Chapman and Pratt 1982). Ca, Mg, Fe, Cu, and Zn were quantified using a Perkin Elmer model 3110 atomic absorption spectrometer (Oliveira *et al.*, 2010). The economic analysis was carried out using direct cost analysis, considering the reduction of costs due to input savings according Corella (2020). Hence, the volume of nutrient solution saved (L ha^{-1}) was multiplied by the average cost of fertilizers (US$ L^{-1}).

Chemical variables of the fruits

Titratable acidity was determined by the method of the Association of Official Analytical Chemists (AOAC; Boland, 1990). Ten grams of fresh fruit pulp were weighed and liquefied with 50 mL of distilled water. Then, an aliquot of 5 mL was titrated with 0.01N NaOH, which was previously added with three drops of phenolphthalein as an indicator. The percentage of titratable acidity (TA) was calculated according to the following equation. The pH was determined in the same extract with an ORION model 701 A potentiometer.

$$TA = \frac{(\text{NaOH } volume\ used)(\text{NaOH } Normality)(mEq\ of\ Acid)(V)}{(sample\ weight)(aliquot\ volume)} \times 100$$

where: *TA* is the percentage of titratable acidity, NaOH volume is given in mL, *mEq* of the acid correspond to the weight of 1 mEq of the acid found in higher proportion in the fruit

(citric acid=0.064), *V* is the volume used for liquefied the fresh fruit, the sample weight is given in g, and the aliquot volume is given in mL.

The content of total soluble solids (TSS) was determined by the method of Boland (1990), which consisted of placing two drops of strawberry fruit juice in a digital refractometer (ATAGO, PAL^{-1} China) previously calibrated with distilled water. The results were reported in Brix degrees (°Brix).

Measurement of soluble sugars in fruit

The extraction of sucrose, glucose, and fructose was conducted according to Ogiwara *et al.* (1999). Ten grams of fresh fruit pulp were liquefied with 50 mL of distilled water. The samples were heated in a microwave oven for 40 s and centrifuged at 12,000 rpm for 10 min. Then, 5 μL of each sample was mixed with 200 μL of a solution composed of 25 mM-HCl HEPES (pH=8.0), 50 mM KCl, 1 mM ATP, 3 mM $MgCl_2$, 0.3 mM NAD, and 1U mL^{-1} yeast hexokinase. Basal absorbance was determined with a microplate reader (Multiskan FC microplate photometer, Thermo Scientific, USA) at 340 nm. In the second stage, 1 U mL^{-1} of glucose 6-phosphate dehydrogenase was added to the mixture, and stable absorbance was determined at 340 nm. For the fructose extraction, 1 U mL^{-1} of phosphoglucose isomerase was added, followed by 1 U mL^{-1} invertase. Glucose and fructose were quantified in the same reaction. In this sequence of reactions, sugars are stoichiometrically transformed to glucose 6-phosphate (G6P) and then to 6-phosphogluconate. The sample concentrations were calculated using the equation from a linear calibration curve created with known concentrations of glucose (5 mM), fructose (5 mM), and sucrose (2.5 mM) (Bernal *et al.*, 2005). Finally, the total sugar concentration included glucose, fructose, and sucrose concentrations.

Photosynthetic pigments

Photosynthetic pigments were measured in the fruiting stage of the strawberry plants. Five circular segments of 5 mm diameter were randomly cut from the mature leaves of the main branch of each experimental unit. The segments were placed in 5 mL of 80% (v/v) acetone. Extraction was performed in the dark at 4 °C until the leaf circles became transparent. The concentration of photosynthetic pigments was determined in a Varian UV-visible spectrophotometer at three wavelengths: 663.2 nm, 646.8 nm, and 470 nm. Carotenoids and chlorophyll content were calculated according to the equations of Lichtenthaler (1987).

$$\text{Chlorophyll } a\left(\text{mg g}^{-1}\right)=\left[\left(12.25\times A_{663.2}\right)-\left(2.79\times A_{646.8}\right)\right]\left[\frac{volume\left(\text{mL}\right)of\ 80\%\ acetone}{weight\left(\text{g}\right)of\ the\ five\ segments}\right]$$

$$\text{Chlorophyll } b\left(\text{mg g}^{-1}\right)=\left[\left(21.50\times A_{646.8}\right)-\left(5.10\times A_{663.2}\right)\right]\left[\frac{volume\left(\text{mL}\right)of\ 80\%\ acetone}{weight\left(\text{g}\right)of\ the\ five\ segments}\right]$$

$$Total\ chlorophyll\left(\mathrm{mg\,g^{-1}}\right)=\left[\left(7.15\times A_{663.2}\right)+\left(18.71\times A_{646.8}\right)\right]\left[\frac{volume\left(\mathrm{mL}\right)of\ 80\%\ acetone}{weight\left(\mathrm{g}\right)of\ the\ five\ segments}\right]$$

$$Carotenoids\left(\mathrm{mg\,g^{-1}}\right)=\left[\frac{\left(\left(1000\times A_{470}\right)-\left(1.82\times A_{Chla}\right)-\left(85.02\times A_{Chlb}\right)\right)}{198}\right]\left[\frac{volume\left(\mathrm{mL}\right)of\ 80\%\ acetone}{weight\left(\mathrm{g}\right)of\ the\ five\ segments}\right]$$

Mycorrhizal colonization

Four representative root samples were obtained for each experimental unit using a hole-punch tool. Strawberry roots were washed and cut into 1 cm segments, which were cold clarified with 3% KOH for 10 d to remove root pigmentation. Then, they were immersed in 3% HCl for 15 min and stained with 0.5% trypan blue in 50% glycerin for three d (Phillips and Hayman, 1970). The percentage of total colonization by AMF was determined according to Koske and Gemma (1989) on permanent preparations of root segments, which were observed under a Leica optical microscope (DM750 model, 40x objective). The frequency of AMF structures was quantified by considering the presence or absence of arbuscules, vesicles, and hyphae. AMF frequency was calculated with the following formula:

$$\%\ total\ colonization=\frac{Number\ of\ colonized\ fields}{Total\ observed\ fields}\times 100$$

Glomalin concentration in the root

For methodological purposes, glomalin is referred in this study as a group of proteins produced by AMF. Total glomalin in the root (TGR) and glomalin in the substrate may improve the substrate structure. However, the organic substrate components interfered with glomalin extraction, resulting in an overestimation of the values (data not shown). Therefore, only TGR was evaluated. Strictly speaking, TGR refers to the concentration of glomalin-like proteins extracted from the root. To measure this concentration, we placed 1 g of root and 8 mL of 20 mM sodium citrate pH=7.0 in 20 mL glass tubes. Subsequently, the samples were sterilized in the autoclave at 121 °C for 1 h. The supernatant volume was measured and stored at 4 °C. Roots remaining at the bottom of the tubes underwent repeated extraction (with 8 mL of sodium citrate and autoclaving) until the reddish-brown color in the samples disappeared. The supernatant of each sample was stored in the same bottle. Finally, the total volume was measured, and the samples were stored at 4 °C (Gonzalez-Chavez *et al*., 2004). Protein concentration was determined using a calibration curve with bovine serum albumin as a standard solution. This solution was prepared from

a 1 mg mL^{-1} solution in saline phosphate buffer at pH=7.4, with Bradford reagent as a dye in a 1:4 ratio with deionized water. Before the assay, the stored extracts were shaken in a vortex for 1 min. Then, 40 μL of Bradford reagent and 160 μL of the protein extract from the roots were added to the microplate trays in triplicate, allowing to react for 1 min, and then shaken (Bradford, 1976). A control sample without protein extract was run simultaneously. The standard calibration curve was linear (R^2=0.9729), with a sensitivity range from 0 to 1 mg mL^{-1}. The absorbance was measured at 595 nm using a microplate reader, and the results were expressed as mg of glomalin per g of root.

Statistical analysis

The experimental data were tested for normality and homogeneity of variance using the Shapiro-Wilks (α=0.05) and Bartlett (α=0.05) tests, respectively. Data that did not meet these assumptions were transformed using the Box-Cox method. The lambda coefficients (λ) obtained in the transformations were: Foliar nitrogen in peatmoss of the Albion strawberry variety (λ=1.9), and in the San Andreas variety (λ=1.4). Foliar potassium in Peatmoss of the San Andreas variety (λ=0.8). Sucrose concentration in Peatmoss of Albion variety (λ=0.15). Water use was analyzed using repeated measures. Before the analysis, the assumptions of normality were corroborated with the Shapiro-Wilks (α=0.05), and homogeneity of variance with the Levene test (α=0.05). A marginal violation of the homogeneity assumption was detected (p=0.045); however, because the experimental design was completely balanced, the ANOVA is considered robust to this deviation, and the validity of the F test is maintained (Box, 1954). Additionally, the sphericity test (Mauchly) showed a significant violation (p=0.012) in the Substrate 1 —San Andreas cultivar. Therefore, the Greenhouse-Geisser correction was applied to the degrees of freedom to validate the F test (Greenhouse & Geisser, 1959).

Analysis of variance, followed by multiple comparisons using Tukey's test (α=0.05) was performed. For the other variables (photosynthetic pigments, leaf and fruit nutrients, °Brix, titratable acidity, soluble sugars, glomalin, and mycorrhizal colonization), we performed an analysis of variance and multiple comparisons of means using Tukey's test (α=0.05). Principal component analysis (PCA) was executed for the following data: micro and macronutrient concentrations in fruit and leaf, chemical variables of the fruits, water use, TGR concentration, photosynthetic pigment concentrations, soluble sugars, and percentage of AMF colonization. The PCA was calculated from a correlation matrix because the measurement scales differed for each variable; therefore, it ensured that all data had the same weight (Greenacre *et al.*, 2022). The applicability of PCA was validated using Bartlett's sphericity test. Statistical analyses were performed with R statistical software version 4.1.1 for Windows.

RESULTS AND DISCUSSION

Water use per strawberry plant

The water use was similar during the first month in both cultivars (Albion and San Andreas), and substrates 1 and 2 (Figure 1). From the second month onward, statistical differences were observed between treatments, in both substrates and cultivars. In

substrate 1, plants of cultivar Albion inoculated with *F. mosseae* Mich had the lowest water use compared to the other treatments from April to August. In cultivar San Andreas, plants inoculated with AMF had the lowest water expenditure in April and May ($\alpha=0.05$). Meanwhile, plants inoculated with *F. mosseae* Mich in June and July showed significantly lower water use than the M. conv and control treatments. Moreover, in August, the water use of the plants inoculated with *F. mosseae* Mich differed from that of the control plants. In substrate 2, during August, September, October, and December, plants of the Albion cultivar inoculated with *F. mosseae* Mich showed the lowest water use compared to those of the M. conv and control treatments. In November, significant differences were only observed in M. conv plants in terms of water use. Meanwhile, during August and October, plants of the San Andreas cultivar inoculated with *F. mosseae* Mich had lower water use compared to M. conv, control, and *F. geosporum* inoculated plants. In September, the water use of plants inoculated with *F. mosseae* Mich was lower than that of plants inoculated with M. conv and those inoculated with *F. geosporum*. In November, plants inoculated with *F. mosseae* Mich had lower water use than plants in the M. conv and control treatments. Finally, in December, plants inoculated with *F. mosseae* Mich had lower water use than plants with the control treatment.

The differences in water use between treatments from the second month onward could be attributed to the functional establishment of the mycorrhizal symbiosis in strawberry plants.

Taylor and Harrier (2001) observed that strawberries established a mycorrhizal symbiosis 25 to 28 d after inoculation. Moreover, Andrade *et al.* (1998) reported that the establishment of AMF in the growth substrate often occurs within the first five to ten weeks. In addition, Augé *et al.* (2001) noted that the influence of AMF on plant physiology becomes significant over time. However, the benefits of this symbiosis are specific and dependent on both cultivars and AMF strains (Sinclair *et al.*, 2014). This could explain why treatments inoculated with *F. geosporum* and *F. mosseae* BEG25 showed different water use than those of plants inoculated with *F. mosseae* Mich.

Overall, *F. mosseae* Mich produced the lowest water use in our strawberry plants. For the Albion cultivar, calculating the total water consumption of the entire six months for each treatment revealed that the plants inoculated with *F. mosseae* Mich in substrate 1 required 5.2 L, 2.2 L, 3.8 L, and 3.5 L less water than the plants inoculated with *F. geosporum*, F. mosseae BEG25, and the M. conv and control treatments, respectively. In cultivar San Andreas, the water savings were 1.9 L, 2.2 L, 5.1 L, and 5.6 L for the same treatments. Moreover, plants inoculated with *F. mosseae* Mich of cultivar Albion in substrate 2 saved 4.5 L, 2.1 L, 6.5 L, and 5.5 L compared to plants inoculated with *F. geosporum* and *F. mosseae* BEG25; whereas cultivar San Andreas saved 6.2 L, 2.9 L, 7.2 L, and 6.8 L compared to plants with M. conv and control treatments.

Some studies have shown that the substrates of AMF-inoculated plants retain more moisture than those of non-inoculated plants, which could decrease water use in plants. Bitterlich *et al.* (2018) observed that *Solanum lycopersicum* plants inoculated with *F. mosseae* increased moisture retention in the growth substrate (sand and vermiculite in a 1:1 v/v ratio) compared to non-inoculated plants. Pauwels *et al.* (2020) demonstrated that *Medicago*

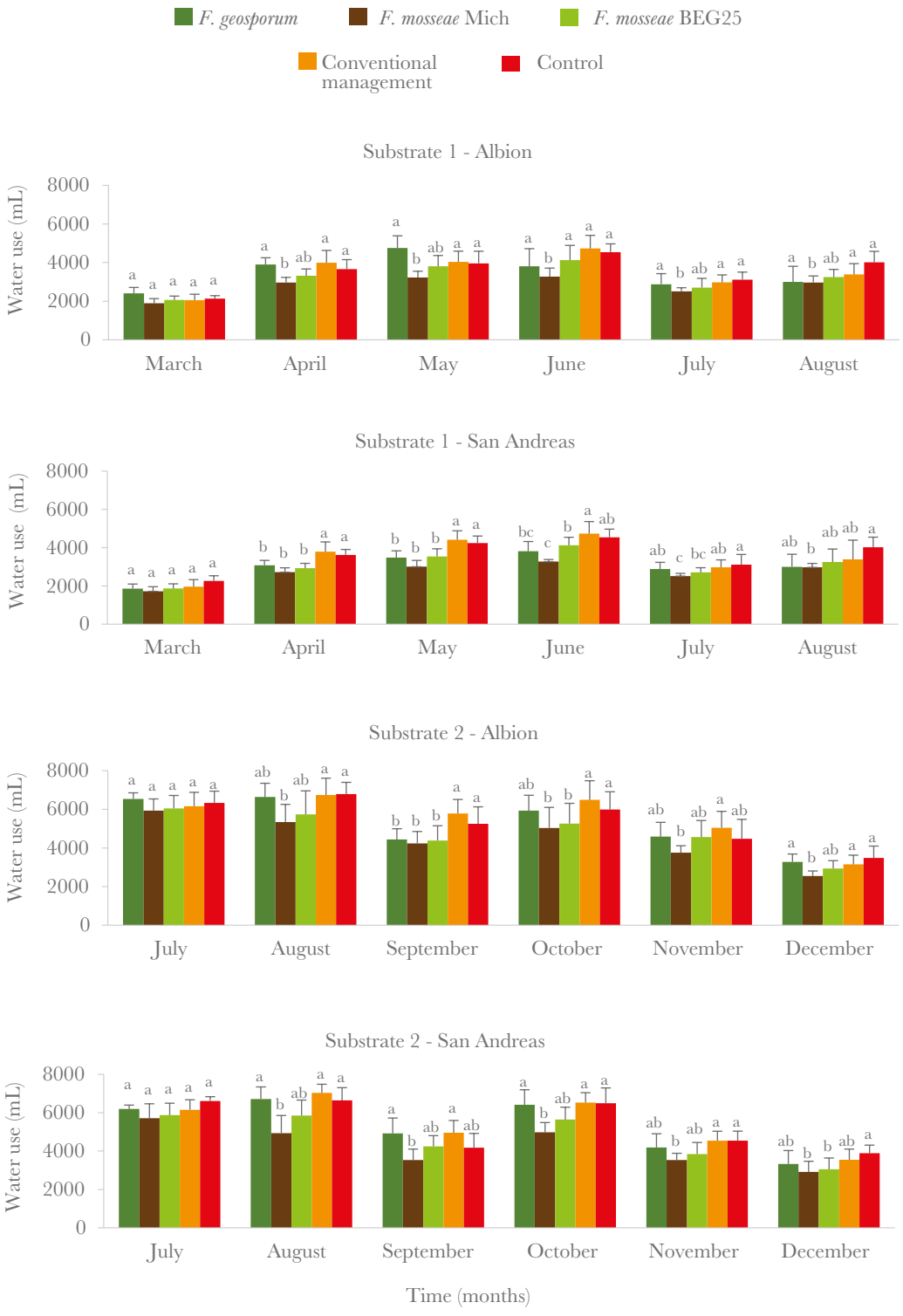

Figure 1. Montly water use during the experiment by two strawberry cultivars grown in two substrates and five treatments n=10. The mean and standard deviation are shown. Different letters indicate significant differences among the five treatments in each evaluation per month.

truncatula plants inoculated with *Rhizophagus irregularis* had higher water retention in a sand and zeolite substrate (1:1 v/v) compared to non-inoculated plants. In both investigations, the authors reported that the higher moisture retention in substrates with inoculated plants is due to the AMF's ability to improve the substrate's structure.

In substrate 1, both strawberry cultivars inoculated with *F. mosseae* Mich had an average water saving of less than 6 L compared to the control over the six-months. In substrate 2, the same treatment saved less than 7 L compared to the control. Under commercial greenhouse conditions for strawberries, the average plant density is 7 per m^2, equivalent to 50,000 plants per ha (Alvarado-Chávez *et al.*, 2020). Based on the water use results from substrate one of the Albion and San Andreas cultivars inoculated with *F. mosseae* Mich, it is estimated that water savings of 38,000 L and 50,000 L, respectively, occur compared to the control. In substrate 2, for the cultivars Albion and San Andreas, water use savings were estimated at 65,000 L and 71,000 L, respectively. These data suggest that AMF can significantly improve water use efficiency in strawberry cultivation. This improvement could be relevant and beneficial under a climate change scenario, where water availability is uncertain. Therefore, the results support that AMF are a viable alternative for efficient water use in agriculture. Since agriculture consumes up to 70% of the water extracted from aquifers (FAO, 2019), plant farmers urgently need this alternative. Future research should address how chemical and physical substrate properties influence AMF establishment, water dynamics, and *viceversa*.

Photosynthetic pigments

In substrate 1, control plants from cultivar Albion presented lower concentrations of chlorophyll *a*, total chlorophyll, and carotenoids compared to the other treatments. This trend was also observed in the San Andreas cultivar, where control plants showed lower chlorophyll *a* and carotenoid concentrations. No significant difference was observed between treatments in chlorophyll *b* concentration in both cultivars (Table 1).

In the Albion cultivar, the average concentration of chlorophyll *a*, total chlorophyll, and carotenoids in the inoculated and M. conv treatments were 53%, 39%, and 38% higher than the control plants. In the cultivar San Andreas, the average concentrations of chlorophyll *a* and carotenoids in the same treatments were 41% and 21% higher compared to the control plants. For total chlorophyll, the two *F. mosseae* isolates exhibited that were at least 36% higher than those of the control plants.

In substrate 2, control plants of the Albion cultivar showed a trend of lower concentrations of chlorophyll *b*, total chlorophyll, and carotenoids. Plants inoculated with the two isolates of *F. mosseae* showed 84% higher chlorophyll *a* concentration than control plants. The average chlorophyll *b*, total chlorophyll, and carotenoid concentrations of the inoculated and M. conv treatments were 37%, 64%, and 46% higher than the control plants. In addition, in the San Andreas cultivar, inoculated plants showed the highest concentration of chlorophyll *b*, total chlorophyll, and carotenoids. On average, the concentrations of the three inoculated treatments were 65%, 73%, and 55% higher than those of the control plants.

Mikiciuk *et al.* (2019) found higher concentrations of chlorophyll *a* (2.63 mg g^{-1}) and total chlorophyll (3.50 mg g^{-1}) in strawberry plants inoculated with *Rhizophagus intraradices*,

Table 1. Chlorophyll *a*, *b*, total and carotenoids concentration (mg g^{-1} FW) in strawberry leaves from two cultivars (Albion and San Andreas) grown in two substrates.

Photosynthetic pigments	Treatments									
	F. geosporum	***F. mosseae* Mich**	***F. mosseae* BEG25**	**Conventional management**	**Control**	***F. geosporum***	***F. mosseae* Mich**	***F. mosseae* BEG25**	**Conventional management**	**Control**
	Substrate 1									
	Albion					**San Andreas**				
Chlorophyll *a*	1.09±0.17 a	1.11±0.19 a	1.08±0.22 a	1.01±0.20 a	0.70±0.22 b	1.09±0.19 a	1.16±0.20 a	1.18±0.22 a	1.11±0.19 a	0.80±0.21 b
Chlorophyll *b*	0.46±0.10 a	0.46±0.06 a	0.49±0.12 a	0.44±0.13 a	0.40±0.01 a	0.48±0.07 a	0.53±0.12 a	0.49±0.15 a	0.46±0.16 a	0.43±0.13 a
Total chlorophyll	1.55±0.25 a	1.57±0.23 a	1.56±0.30 a	1.45±0.22 a	1.10±0.27 b	1.57±0.21 b	1.68±0.28 a	1.67±0.30 a	1.56±0.27 b	1.23±0.28 c
Total Carotenoids	0.37±0.06 a	0.40±0.07 a	0.39±0.11 a	0.34±0.11 a	0.27±0.08 b	0.40±0.11 a	0.44±0.13 a	0.41±0.07 a	0.40±0.08 a	0.34±0.08 b
	Substrate 2									
	Albion					**San Andreas**				
Chlorophyll *a*	1.20±0.18 b	1.24±0.24 ab	1.31±0.22 a	1.19±0.20 b	0.69±0.27 c	1.30±0.19 a	1.31±0.22 a	1.32±0.28 a	1.10±0.15 a	0.74±0.30 b
Chlorophyll *b*	0.52±0.13 a	0.53±0.09 a	0.55±0.13 a	0.49±0.12 a	0.38±0.12 b	0.50±0.09 a	0.51±0.10 a	0.48±0.11 ab	0.42±0.11 b	0.30±0.10 c
Total chlorophyll	1.71±0.25 a	1.77±0.27 a	1.86±0.28 a	1.68±0.25 a	1.07±0.24 b	1.80±0.26 a	1.82±0.30 a	1.80±0.32 a	1.52±0.22 b	1.04±0.21 c
Total Carotenoids	0.57±0.11 a	0.59±0.13 a	0.62±0.13 a	0.57±0.11 a	0.40±0.09 b	0.67±0.12 a	0.65±0.11 a	0.63±0.13 ab	0.56±0.10 b	0.42±0.10 c

Table shows average and standard deviation from 5 replicates. Different letters represent a statistical difference in photosynthetic pigment for each treatment, according to the Tukey test ($\alpha = 0.05$).

compared to the chlorophyll *a* concentration in our strawberry plants. However, the carotenoid concentration (0.39 mg g^{-1}) is comparable to our results with both strawberry varieties in substrate 2.

Furthermore, Lachinani *et al.* (2023) observed even higher concentrations of chlorophyll *a* (7.11 mg g^{-1}), chlorophyll *b* (5.76 mg g^{-1}), total chlorophyll (12.87 mg g^{-1}), and carotenoid concentration (3.22 mg g^{-1}) in strawberry plants inoculated with *R. irregularis*. Other studies have observed an increase in chlorophyll *a*, concentration, total concentration, and carotenoid concentration in inoculated strawberry plants compared to control plants. Baslam *et al.* (2013) explained this observation on the basis that AMF stimulate metabolic pathways responsible for synthesizing these pigments. Photosynthetic pigment synthesis is known to have a positive correlation with nutrients (Khan *et al.*, 2022). In agreement with this, our plants in the M. conv treatment received 40% more nutrient solution compared to the plants with other treatments. The increase in chlorophyll *a* and carotenoids is particularly beneficial for strawberry plants because chlorophyll *a* converts solar energy into chemical energy through electron transfer (Luo *et al.*, 2022), which increases plant metabolism and improves growth and photosynthetic rate (Khan *et al.*, 2022). Conversely, carotenoids can promote resistance to biotic and abiotic stresses in plants (Vafadar *et al.* 2014). Therefore, inoculated plants have better metabolic conditions since they show higher concentrations of photosynthetic pigments.

Foliar nutrient concentration

Similar to photosynthetic pigment concentrations, both cultivars in substrate 1 had lower macronutrient and micronutrient concentrations in the control, except for Fe (Table 2). In the Albion cultivar, the highest foliar P concentration was found in inoculated plants (average of 714.1 mg kg^{-1} dry weight) compared to M. conv (479.8 mg kg^{-1}) and control plants (293.7 mg kg^{-1}). In the San Andreas cultivar, the average leaf concentration in inoculated plants was similar to that of plants with M. conv (747 mg kg^{-1}) but higher than control plants (304 mg kg^{-1}). Plants of cultivar Albion inoculated with *F. mosseae* BEG25 had an N concentration 71% higher than control plants and 4% higher than plants with M. conv. In cultivar San Andreas, plants inoculated with *F. mosseae* BEG25 had 85% higher leaf N concentration, while M. conv plants had 64% higher leaf N concentration, this compared to control plants. In the Albion cultivar, the plants inoculated with *F. mosseae* BEG25 and M. conv increased their K leaf concentration by 42% on average compared to the control, while in the San Andreas cultivar, the increase was 32%. In addition, within the same cultivar and under the same treatments, we observed a 79% increase in leaf Mg concentration compared to the control plants. However, in the San Andreas cultivar, the plants inoculated with *F. mosseae* BEG25 showed the highest increase in foliar Mg (119%) compared to the control plants and those inoculated with *F. geosporum*.

In the Albion cultivar, the foliar Ca concentration was 57% higher in plants with the M. conv treatment compared to control plants, while in the cultivar San Andreas with the same treatment, the foliar Ca concentration was 31% higher than in control plants. In both cultivars, the leaf concentrations of Zn and Mn were similar between treatments but higher than those of the control plants. Moreover, in the Albion cultivar, the lowest leaf

Table 2. Effect of five treatments in the concentration of micro- and macronutrients in the leaves of strawberry plants grown in two substrates

Nutrients	Treatments									
	F. geosporum	*F. mosseae* Mich	*F. mosseae* BEG25	Conventional management	Control	*F. geosporum*	*F. mosseae* Mich	*F. mosseae* BEG25	Conventional management	Control
	Substrate 1									
	Albion					San Andreas				
N (%)	2.0±0.2 b	2.0±0.3 b	2.4±0.1 a	2.3±0.2 ab	1.4±0.2 c	2.5±0.6 a	2.0±0.6 b	2.6±0.2 a	2.3±0.2 ab	1.4±0.5 b
P (mg kg^{-1})	786±110 a	739±141 a	616±88 ab	480±45 b	294±82 c	853±138 a	623±92 a	614±87 a	747±195 a	304±76 b
K (g kg^{-1})	20.4±2 b	18.6±3 b	25.6±3 a	22.1±2 a	16.7±2 c	20.3±2 b	22.4±3 a	23.5±3 a	21.0±3 a	16.8±2 c
Ca (g kg^{-1})	15.0±1 b	15.0±2 b	16.6±1 ab	19.6±2 a	12.5±0.6 c	15.1±1 a	14.9±2 a	15.1±3 a	16.6±4 a	12.6±1 b
Mg (g kg^{-1})	6.2±1 b	6.6±1 b	9.4±2 a	9.7±1 a	5.3±1 c	6.0±1 c	7.4±1 b	11.2±3 a	7.3±2 b	5.1±1 c
Cu (mg kg^{-1})	8.5±1 a	7.1±1 ab	10.0±2 a	9.9±2 a	1.6±0.5 c	4.9±1 b	6.5±2 a	12.2±5 a	7.2±3 a	2.1±1 c
Mn (mg kg^{-1})	79.9±13 a	103.2±12 a	106.5±23 a	98.1±28 a	51.9±12 b	90.9±22 a	85.1±17 a	110.0±28 a	101.7±22 a	44.4±17 b
Fe (mg kg^{-1})	189.7±26 a	185.3±30 a	209.5±35 a	178.1±11 a	178.3±12 a	184.0±42 a	213.5±63 a	193.7±63 a	201.4±35 a	185.9±44 a
Zn (mg kg^{-1})	91.3±4 a	92.6±10 a	100.9±18 a	96.8±12 a	53.6±5 b	92.4±22 a	92.8±18 a	124.1±23 a	96.9±9 a	60.6±9 b
	Substrate 2									
	Albion					San Andreas				
N (%)	2.0±0.1 b	2.0±0.2 b	2.3±0.2 a	2.0±0.1 b	1.0±0.1 c	2.1±0.2 a	2.2±0.4 a	2.0±0.1 a	2.0±0.1 a	1.1±0.1 b
P (mg kg^{-1})	665±53 a	582±56 a	604±49 a	613±55a	347±70 b	615±61 a	632±82 a	680±44 a	665±76 a	419±52 b
K (g kg^{-1})	24.0±2 ab	23.2±1 ab	26.2±1 a	23.5±1 ab	20.3±1 b	24.1±2.4 a	25.1±1.5 a	26.9±1.4 a	24.5±1.6 a	19.2±1.4 b
Ca (g kg^{-1})	9.2±0.6 ab	10.6±1 a	11.0±0.7 a	11.8±0.2 a	8.7±0.4 b	10.3±0.2 b	10.0±0.3 b	11.3±0.6 a	11.8±1 a	8.4±1.3 c
Mg (g kg^{-1})	5.9±0.3 b	6.0±0.9 ab	6.2±1.0 ab	7.4±0.7 a	3.2±0.8 c	6.3±0.4 a	5.9±0.8 ab	6.6±0.4 a	6.0±0.2 ab	4.3±1.8 b
Cu (mg kg^{-1})	4.2±0.7 b	5.2±0.6 a	6.9±2.0 a	4.9±1.0 b	2.7±1.0 c	3.7±0.5 b	4.2±0.7 b	6.2±0.9 a	4.4±0.7 b	2.5±0.1 c
Mn (mg kg^{-1})	65.6±2 a	65.2±3 ab	69.5±2 a	66.2±3 a	60.6±3 b	65.3±2 b	65.2±1 b	69.7±2 a	65.3±1 b	57.4±1 c
Fe (mg kg^{-1})	149.8±5 a	158.6±12 a	161.0±6 a	159.4±13 a	135.0±6 b	166.2±15 a	168.4±14 a	171.8±8 a	164.0±17 a	141.7±14 b
Zn (mg kg^{-1})	61.1±2 b	59.2±1 b	66.8±1 a	60.8±1 b	52.6±4 c	57.1±2 b	57.8±2 ab	61.1±3 a	56.7±1 b	49.3±2 c
Reference values*										
N (%)	2.0 - 3.0	P (mg kg^{-1})	3000 - 4000	K (g kg^{-1})	13 - 18	Ca (g kg^{-1})	10 - 22	Mg (g kg^{-1})	2.8 - 4.2	
Cu (mg kg^{-1})	2.6 - 4.9	Mn (mg kg^{-1})	65 - 320	Fe (mg kg^{-1})	85 - 200	Zn (mg kg^{-1})	11 - 20			

n=5. Different letters show a statistical difference in nutrients concentration between treatments, based on the Tukey test (α=0.05). *Reference nutrient values for strawberry leaves according to Bolda *et al.* (2012).

Cu concentration was observed in control plants; conversely, in the San Andreas cultivar, the lowest concentration corresponded to control plants and plants inoculated with *F. geosporum*.

In substrate 2, all control plants of both cultivars had the lowest foliar concentration of nutrients evaluated. Treated plants in the Albion and San Andreas cultivars had, on average, 77% and 54% higher P concentrations than control plants, respectively. The same trend was observed in the San Andreas cultivar regarding the foliar concentrations of K and N; the treated plants, whether inoculated or treated with M. conv, had 30% and 88% more of these nutrients. Moreover, in the Albion cultivar, the plants inoculated with *F. mosseae* BEG25 had the highest concentration of K (26.2 mg kg^{-1}) and N (2.3%). Plants treated with M. conv and inoculated with *F. mosseae* BEG25 had a higher average leaf Ca concentration (11.4 mg kg^{-1}) than control plants (8.7 mg kg^{-1}). In the San Andreas cultivar, the same treatments resulted in an average Ca concentration of 11.5 mg kg^{-1}, while the control had 8.4 mg kg^{-1}. Plants inoculated with *F. mosseae* BEG25 had higher leaf Zn concentrations than control plants, 26% more in the Albion cultivar and 23% more in the San Andreas. In the Albion cultivar, the highest leaf concentration of Mn was observed in plants inoculated with *F. mosseae* BEG25 and M. conv, while the highest leaf concentration of Cu was found in plants inoculated with both mycorrhizal isolates of *F. mosseae*. In contrast, in the San Andreas cultivar, plants inoculated with *F. mosseae* BEG25 had the highest leaf concentrations of Cu and Mn, 148% and 21% higher, respectively, than control plants. Finally, the foliar concentration of Fe for both cultivars was 16% higher in treated plants compared to control plants.

Other authors have also observed higher concentrations of certain nutrients in inoculated strawberry plants compared to non-inoculated plants. Haghshenas *et al.* (2024) found higher concentrations of P (5,300 mg kg^{-1}), K (27 g kg^{-1}), and N (2.86%) in the leaves of strawberry plants inoculated with *Glomus mosseae* (currently, *F. mosseae*) compared to control plants. Taylor and Harrier (2001) quantified higher concentrations of Cu (9 mg kg^{-1}), Mn (391 mg kg^{-1}), and Zn (33 mg kg^{-1}) in the leaves of strawberry plants colonized with *Glomus clarum* (currently, *Rhizophagus clarus*) compared to non-inoculated plants. Regarding the leaf concentration of Ca and Mg, the present investigation is one of the first to demonstrate differences in these elements in AMF-inoculated strawberry leaves, highlighting the importance of mycorrhization in the increased absorption of these macronutrients.

Based on the reference values reported by Bolda *et al.* (2012; Table 2), the control plants show foliar N and Mn deficiencies in both cultivars and substrates, but Cu deficiency in the Albion cultivar in both substrates. For the San Andreas cultivar, only substrate 2 had Cu deficiency. Ca deficiencies were also observed in control plants of both cultivars growing in substrate 2. These data show that strawberry plants responded favorably to inoculation and the M. conv treatment. Regarding leaf P concentration, inoculated and M. conv plants had higher P concentrations than control plants ($\alpha = 0.05$) in both substrates and cultivars. However, the P concentration in all treatments was lower than the reference value of 3000 mg kg^{-1}; this could result from all treatments being irrigated with a Hoagland solution low in phosphorus.

The higher concentration of nutrients in treatments inoculated with *F. mosseae* and *F. geosporum* is due to AMF facilitating the absorption of these nutrients by plants (Khaliq *et al.*, 2022). Nutrient absorption is essential for plant growth since an adequate concentration of nutrients in leaves is crucial for optimal plant development (Trejo-Téllez and Gómez-Merino, 2014). It is worth noting that although the M. conv treatment included the application of 40% more nutrient solution, the nutritional quality of the plants was not higher than that of plants inoculated with *F. mosseae* Mich. In addition, as mentioned earlier, the treatment inoculated with *F. mosseae* Mich saved up to 7 L of Hoagland solution compared to M. conv during the period evaluated. Based on fertilizer prices for Mexico in 2023, we estimated savings of US$0.0027 per 7 L of nutrient solution. Hence, the potential input saving for substrate 1 was estimated to be US$292 ha^{-1} for the Albion cultivar and US$304 ha^{-1} in the San Andreas cultivar. For substrate 2, the projected savings were US$461 and US$440 ha^{-1}, respectively. This estimation was based on direct cost analysis and assuming a density of 50,000 plants ha^{-1}, which occurs in the commercially strawberry production.

Nutritional analysis of strawberry fruits

Fruit Fe concentration was similar in plants from both cultivars and substrates. The highest fruit P concentration was observed in plants from the M conv treatment in both cultivars and substrates (Table 3). In the Albion cultivar with substrate 1, the concentration of Mg, Mn, Zn, and N was similar in all fruits except those obtained from control plants, which had the lowest concentration of these nutrients. The highest concentrations of Ca and K were observed in plants inoculated with *F. mosseae* BEG25. In the Albion cultivar with substrate 2, there were no differences between treatments for Mg, Mn, and Ca concentrations, except for the fruits of control plants, which presented the lowest concentrations of these nutrients. Also, the highest Zn concentration was observed in fruits from plants inoculated with *F. mosseae* BEG25 and M. conv. The highest concentration of K was observed in fruits from plants inoculated with the two isolates of *F. mosseae*. Fruits from plants inoculated with *F. geosporum*, *F. mosseae* BEG25, and M. conv had the highest N content. The highest P concentration was observed in plants of the Albion cultivar under the M. conv treatment in both substrates. Similar Zn and Ca concentrations were observed in the fruit across all treatments in the San Andreas cultivar with substrate 1, except for the control plants.

The N fruit content was also similar among treatments, but was lower in the control plants. In substrate 1, the highest concentration of Mg in the fruit was observed in plants inoculated with *F. mosseae* BEG25. In contrast, the K concentration was similar in the fruit of plants inoculated with the two isolates of *F. mosseae* and M. conv. In the San Andreas cultivar with substrate 2, the fruits of plants inoculated with *F. mosseae* BEG25 and M. conv had the highest concentration of Mg and K.

In general, we found positive effects on strawberry fruit nutrition due to the inoculation with *Funneliformis* isolates, resulting from AMF's role in increasing the nutritional quality of fruits (Castellanos-Morales *et al.*, 2010; Mikiciuk *et al.*, 2019). Parada *et al.* (2019) observed higher concentrations of K (60.3 g kg^{-1}) and Mg (13.7 g kg^{-1}) in fruits from strawberry

Table 3. Concentration of macro and micronutrients in strawberry fruits of two cultivars (Albion and San Andreas) grown in two substrates.

Nutrients	Treatments									
	F. geosporum	***F. mosseae* Mich**	***F. mosseae* BEG25**	**Conventional management**	**Control**	***F. geosporum***	***F. mosseae* Mich**	***F. mosseae* BEG25**	**Conventional management**	**Control**
	Substrate 1									
	Albion					**San Andreas**				
N (%)	0.9±0.1 a	0.9±0.1 a	0.9±0.1 a	1.0±0.1 a	0.6±0.0 b	0.8±0.1 a	0.8±0.1 a	0.9±0.1 a	0.9±0.1 a	0.6±0.1 b
P (mg kg^{-1})	106±23 c	133±32 bc	160±13 ab	181±37 a	40±14 d	106±22 b	140±35 b	168±46 ab	163±35 a	35±14 c
K (g kg^{-1})	15.1±2 c	16.1±1 bc	20.2±3 a	19.0±2 ab	12.7±1 d	15.4±2 b	20.7±3 a	22.2±4 a	19.2±1 a	12.2±2 c
Ca (g kg^{-1})	2.2±0.5 b	2.6±0.5 ab	3.6±0.6 a	3.3±1.2 ab	1.5±0.4 b	2.4±0.6 a	2.0±0.4 a	2.5±0.8 a	2.4±0.6 a	1.4±0.3 b
Mg (g kg^{-1})	1.5±0.1 a	1.5±0.1 a	1.7±0.1 a	1.6±0.1 a	1.1±0.1 b	1.6±0.1 b	1.5±0.1 bc	1.8±0.1 a	1.7±0.1 ab	1.3±0.2 c
Mn (mg kg^{-1})	30.0±7 a	32.7±6 a	40.5±13 a	47.5±10 a	21.5±8 b	30.4±2 bc	37.4±3 b	45.0±8 a	46.0±13 a	20.6±10 c
Fe (mg kg^{-1})	28.4±6 a	32.1±4 a	35.3±4 a	29.3±6 a	23.5±5 a	36.7±4 a	42.2±7 a	45.5±8 a	36.2±6 a	26.3±2 a
Zn (mg kg^{-1})	17.7±4 a	16.0±3 a	20.7±2 a	19.0±5 a	10.0±1 b	17.8±5 a	16.8±4 a	19.4±6 a	17.7±6 a	8.4±3 b
	Substrate 2									
	Albion					**San Andreas**				
N (%)	1.0±0.1 a	0.8±0.1 b	1.0±0.1 a	1.0±0.1 a	0.5±0.1 c	1.2±0.2 a	1.3±0.1 a	1.3±0.2 a	1.3±0.1 a	0.7±0.1 b
P (mg kg^{-1})	120±27 c	129±28 b	159±21 b	239±27 a	70±42 c	129±27 b	137±25 b	149±35 b	219±42 a	87±28 c
K (g kg^{-1})	23.2±0.4 b	24.4±0.8 a	24.9±0.5 a	24.2±0.6 ab	18.3±0.4 c	24.3±0.4 b	24.8±0.7 b	26.2±0.4 a	26.0±0.5 a	19.2±0.5 b
Ca (g kg^{-1})	2.2±0.3 a	2.1±0.0 a	2.4±0.2 a	2.2±0.3 a	1.6±0.0 b	2.0±0.1 b	1.9±0.1 b	2.5±0.1 a	2.1±0.1 b	1.5±0.3 c
Mg (g kg^{-1})	2.0±0.1 a	1.7±0.2 a	2.1±0.1 a	2.0±0.2 a	1.2±0.2 b	2.4±0.3 ab	2.2±0.1 b	2.5±0.2 a	2.6±0.2 a	1.5±0.2 c
Mn (mg kg^{-1})	38.7±1 a	39.6±2 a	40.2±1 a	41.3±3 a	30.5±2 b	41.2±1 a	38.7±1 b	41.3±1 a	40.3±1 ab	33.6±1 c
Fe (mg kg^{-1})	30.5±3 a	30.2±1 a	31.2±1 a	30.1±4 a	28.7±1 a	27.6±2 a	28.8±2 a	28.9±2 a	29.7±3 a	27.3±3 a
Zn (mg kg^{-1})	32.7±1 ab	29.6±2 b	35.9±1 a	34.0±5 a	24.3±4 c	32.1±3 ab	31.5±0 b	36.0±2 a	34.3±3 ab	24.5±2 c
Reference values[+]										
N (%)	1	P (mg kg^{-1})	2500	K (g kg^{-1})	17.5	Ca (g kg^{-1})	1.84			
Mg (g kg^{-1})	1.35	Mn (mg kg^{-1})	40	Fe (mg kg^{-1})	28.26	Zn (mg kg^{-1})	11.9			

n=5. Different letters indicate significant differences when comparing nutrient concentrations between treatments. [+]Reference values were estimated from element concentrations in fresh-weight strawberries (USDA 2023), assuming that 100 g of fresh weight contains 90.8% water.

plants inoculated with *Claroideoglomus claroideum* compared to fruits from plants without inoculation. Castellanos-Morales *et al.* (2010) showed higher concentrations of K (185 g kg^{-1}) and Cu (2.8 mg kg^{-1}) in strawberry fruits that were inoculated with *Glomus intraradices* (currently, *R. intraradices*) compared to fruits from uninoculated plants. Importantly, the present study is one of the first to report higher concentrations of Mn, Zn, Ca, and N in fruit from strawberry plants inoculated with AMF compared to non-inoculated plants. Fruit from plants inoculated with *F. geosporum*, *F. mosseae* Mich, *F. mosseae* BEG25, and M. conv had higher concentrations of Fe, Zn, Ca, and Mg than reference values (USDA, 2023), 1.3, 1.7, 1.7, 1.9, and 1.3 times, respectively.

In both substrates and cultivars, only plants from the *F. mosseae* BEG25 and M. conv treatments exceeded the reference fruit Mn concentration, with 1.2 times the value. Similarly, K concentration in fruit was higher than the reference value in plants inoculated with *F. mosseae* BEG25 and M. conv of the Albion cultivar. The concentration of K was also higher in plants inoculated with *F. mosseae* Mich in the cultivar San Andreas with substrate 1. In substrate 2, the concentrations of Fe, Zn, Ca, Mg, and K in the AMF-inoculated treatments and the M. conv treatment were at least 1.2, 3.0, 1.3, 1.5, and 1.4 times higher compared to the values reported in the USDA. Regarding the San Andreas cultivar, the concentrations of these elements were at least 1.1, 3.3, 1.4, 1.9, and 1.5 times higher than those in other cultivars, respectively.

A higher concentration of nutrients in strawberry fruits increases their nutritional value and makes them potentially beneficial for consumer health. Nutrients from strawberry fruits perform specific functions in the body. For example, Fe is involved in the synthesis of deoxyribonucleic acid, as well as electron and oxygen transport (Abbaspour *et al.*, 2014). At the cellular level, Zn is critically involved in proliferation, differentiation, and apoptosis (Costa *et al.*, 2023). Ca is indispensable for the growth and development of an optimal skeletal structure (Ciosek *et al.*, 2021), while Mg is necessary for energy metabolism, as well as muscle contraction and relaxation (Ciosek *et al.*, 2021). Maintaining a diet rich in K helps reduce cardiovascular disease mortality (Muiesan *et al.*, 2023). Therefore, the knowledge generated in this study regarding the impact of AMF inoculation on strawberry fruit nutrition is relevant for producing more nutritious food to promote human health.

Physical and chemical components of the fruit

In addition to the visual appearance of strawberry fruits, chemical components such as sweetness and acidity are important variables that influence consumer preference (Cecatto *et al.*, 2013). In both cultivars and substrates, fruits from strawberry plants with M. conv and inoculated with AMF presented higher citric acid percentages and °Brix compared to the fruits of control plants ($\alpha = 0.05$; Table 4). Cordeiro *et al.* (2019) observed that higher °Brix and citric acid percentages in strawberry fruits were positively correlated with better plant nutrition and higher photosynthetic yield, which was corroborated in the present investigation. Todeschini *et al.* (2018) observed that citric acid concentration (0.46%) was higher in fruits of plants inoculated with *R. irregularis* compared to non-inoculated plants. In the cultivar Camino Real, Cordeiro *et al.* (2019) quantified a 1.2 times higher percentage of citric acid with respect to control plants

Table 4. Effect of five treatments in citric acid content, pH and Brix degrees of fruits of two strawberry cultivars grown two substrates.

Chemical composition	Treatments									
	F. geosporum	***F. mosseae* Mich**	***F. mosseae* BEG25**	**Conventional management**	**Control**	***F. geosporum***	***F. mosseae* Mich**	***F. mosseae* BEG25**	**Conventional management**	**Control**
	Substrate 1									
	Albion					**San Andreas**				
Citric acid (%)	1.14±0.1 a	1.23±0.1 a	1.15±0.2 a	1.18±0.2 a	0.84±0.1 b	1.14±0.2 a	1.12±0.1 a	1.23±0.1 a	1.12±0.1 a	0.83±0.1 b
pH	3.29±0.1 b	3.30±0.1 b	3.32±0.0 b	3.38±0.1 ab	3.42±0.0 a	3.26±0.1 b	3.30±0.1 b	3.29±0.1 b	3.33±0.1 ab	3.42±0.0 a
° Brix	7.52±0.3 a	7.86±0.2 a	7.63±0.4 a	7.93±0.5 a	6.46±0.4 b	7.98±0.3 a	7.78±0.6 a	8.14±0.6 a	7.73±0.4 a	6.49±0.4 b
	Substrate 2									
	Albion					**San Andreas**				
Citric acid (%)	1.15±0.1 a	1.04±0.1 a	1.09±.1 a	1.08±0.1 a	0.85±0.1 b	1.13±0.1 a	1.13±0.0 a	1.18±0.0 a	1.11±0.1 a	0.97±0.1 b
pH	3.91±0.1 b	3.94±0.1 b	3.97±0.1 b	3.96±0.1 b	4.14±0.1 a	3.95±0.1 b	4.02±0.1 ab	3.94±0.1 b	3.91±0.2 b	4.18±0.1 a
° Brix	7.80±0.2 a	7.88±0.1 a	7.98± 0.1 a	8.00±0.4 a	6.94±0.4 b	8.00±0.1 a	8.02±0.2 a	8.00±0.2 a	7.96±0.2 a	7.52±0.2 b

n=5. Different letters show a statistical difference between treatments, based on the Tukey test (α=0.05)

when strawberry plants were inoculated with a consortium of eight AMF species. A higher concentration of citric acid in strawberry fruits benefits human health because it is associated with antioxidant and anti-inflammatory effects in cells (Singh *et al.*, 2022). Importantly, fruits from inoculated plants or plants treated with M. conv presented an ideal °Brix content (≥7%) for foods that have not been modified since harvest (Cecatto *et al.*, 2016). Ansari *et al.* (2018) recorded an increase in °Brix (12%) in strawberry fruits obtained from plants inoculated with *R. intraradices* compared to strawberry fruits from non-inoculated plants (4%). Most consumers prefer strawberries with higher °Brix, as this increases the sweetness of the fruit (Cecatto *et al.*, 2013).

Fruit pH differed between treatments (α=0.05). In general, we observed that in the two substrates and cultivars, fruits from inoculated and M. conv treated plants were more acidic than those from control plants. Similar results were reported by Cekic and Yilmaz (2011), Bona *et al.* (2015), and Todeschini *et al.* (2018). According to Cordeiro *et al.* (2019), fruit with a lower pH is better appreciated by consumers who prefer acidic fruits. Although strawberries contain citric, malic, ellagic, and salicylic acid, Zhang *et al.* (2021) indicated that citric acid is responsible for approximately 92% of the total acidity. This was corroborated by the fact that the treatments with the highest concentration of citric acid also had the most acidic fruit.

In both substrates and cultivars, significant differences were observed in glucose and total sugars (α=0.05); the fruits of control plants had the lowest concentrations (Figure 2). Fruits from plants inoculated with *F. mosseae* BEG25 in cultivars Albion and San Andreas with substrate 1 had the highest concentration of glucose (29.5 and 28.5 mg g^{-1}, respectively) and total sugar (53.3 and 57.1 mg g^{-1}, respectively); this in comparison with control plants. Contrary to control plants, plants inoculated with *F. mosseae* BEG25 in substrate 2 from the Albion cultivar presented the highest concentrations of glucose and total sugar in the fruit which were 29.78 and 53.50 mg g^{-1}, respectively.

In the San Andreas cultivar, the highest glucose concentration (29.24 mg g^{-1}) was observed in fruit from plants inoculated with *F. mosseae* BEG25, while the fruits from plants with M. conv treatment had a higher total sugar concentration (52.80 mg g^{-1}) in both cases compared with fruits from non-inoculated plants.

Bona *et al.* (2015) reported that strawberry plants inoculated with a consortium of five AMF increased their fruit sucrose (10.86 mg g^{-1}) and total sugar (70 mg g^{-1}) content compared to fruits from non-inoculated plants (1.35 and 1.20 times, respectively). In contrast, Castellanos-Morales *et al.* (2010) observed no significant differences in the concentration of glucose, fructose, and sucrose in strawberries from plants either inoculated with *G. intraradices* (currently, *R. intraradices*) or non-inoculated. The differences in strawberry fruit sugar concentrations in inoculated *vs.* non-inoculated plants can be attributed to the influence of AMF species on the metabolic pathways of sugars (Azcón-Aguilar and Barea, 1992; Wang and Wu, 2023); sugar exchange between the plant and the fungus modifies carbohydrate metabolism in the plant and its storage in the fruit (Noceto *et al.*, 2021). Plants inoculated with *F. mosseae* BEG25 showed similar concentrations of sugars in the fruit of plants with the M. conv treatment. This demonstrates that plants inoculated with this fungus promoted sugars production in the

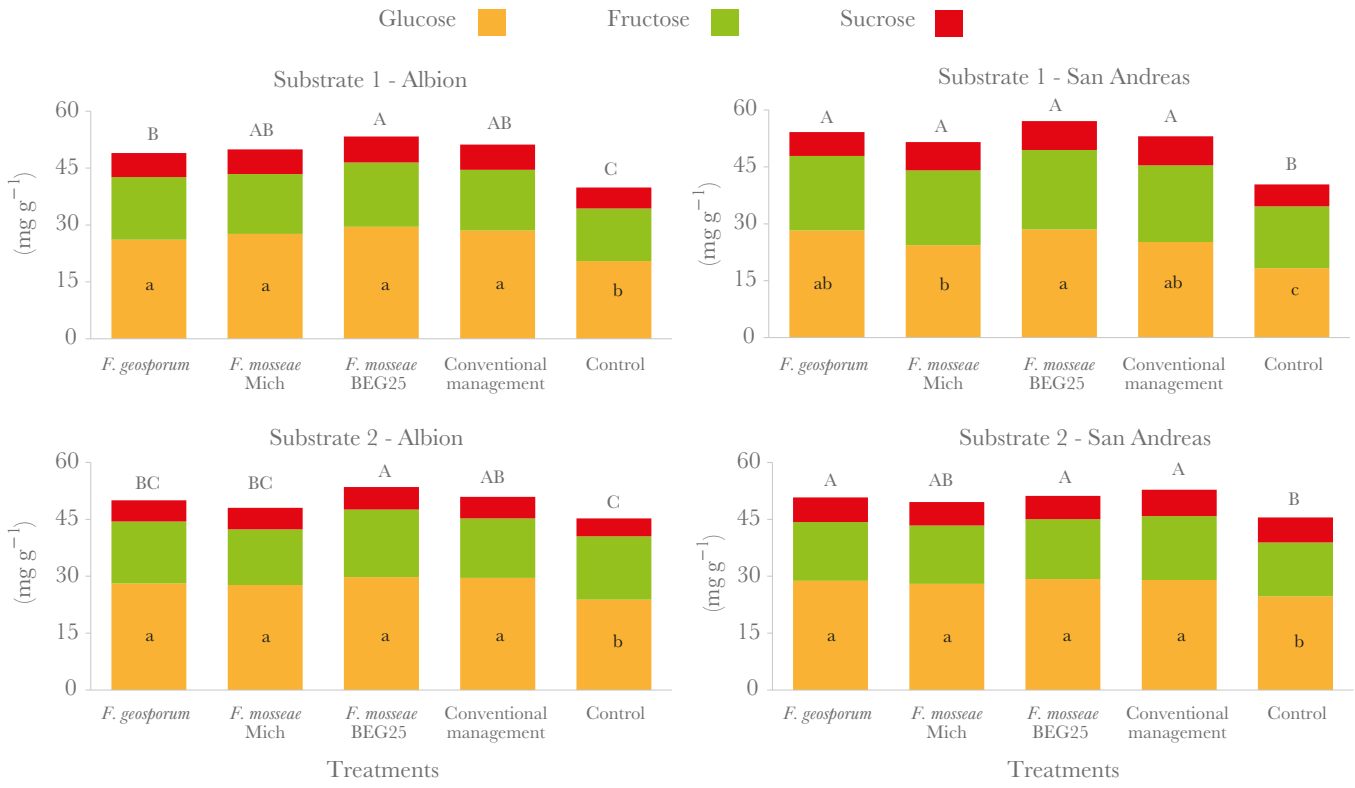

Figure 2. Concentrations of glucose, fructose, sucrose, and total sugar in fruits of two strawberry cultivars grown in two substrates and five treatments, n=5. Lowercase letters show differences between glucose concentrations, and uppercase letters indicate differences in total sugar concentration. No significant differences were observed between fructose and sucrose concentrations.

strawberry fruit, even though the inoculated plants received 40% less nutrient solution. Haghshenas *et al.* (2024) also observed that the nutrient solution strength in the control plants can increase the concentration of sugars in the fruit of strawberry plants and behave similarly to inoculated plants.

Mycorrhizal colonization

AMF colonized all the roots of our inoculated plants, while control plants showed no mycorrhizal structures. Hyphae and vesicles were observed on the strawberry roots, regardless of the cultivar and substrate. For substrate 1, plants from the Albion cultivar showed a colonization interval of 35-37%, while those from the San Andreas cultivar had a colonization interval of 31- 39%. Conversely, in substrate 2, the interval was 35-37% in the Albion cultivar and 36-37% in the San Andreas cultivar. These percentages are within the range reported by Taylor and Harrier in strawberries (2001), which indicates 20-40% of mycorrhizal colonization with *G. clarum* (currently, *R. clarus*). However, other studies with strawberry plants have reported higher percentages of colonization. Robinson-Boyer *et al.* (2016) quantified 55% of colonization with *F. mosseae*. Castellanos-Morales *et al.* (2010) observed a colonization interval of 65-80% with *G. intraradices* (currently, *R. intraradices*). The different colonization percentages could be associated with nutrient availability and environmental conditions specific to each study. In addition, colonization

depends on the AMF species that colonize the roots (Taylor and Harrier, 2001), which can lead to differences even in the same strawberry variety. Importantly, the percentage of colonization is not a direct indication of mycorrhizal benefits (Wang *et al.*, 2023). Although the colonization percentages found in the present study were within the range reported by other authors, it is necessary to acknowledge that the benefits of mycorrhizal colonization depend on several factors. Proper management and optimal conditions may potentiate the benefits of symbiosis.

Total glomalin concentration in roots

In both cultivars and substrates, the roots of plants inoculated with *F. mosseae* Mich presented higher TGR concentration (α=0.05) than other inoculated plants (Figure 1S). In contrast, no TGR was detected in the roots of M. conv treatment and control plants. This is the first study reporting TGR measurement in strawberries; however, Wu *et al.* (2016) showed that root glomalin production varies among mycorrhizal species due to physiological differences and different colonization strategies. Wu *et al.* (2016) found 0.06 mg g^{-1} of TGR in trifoliate orange tree roots inoculated with *F. mosseae*. Singh *et al.* (2013) noted that glomalin production benefits soil structure and positively affects the host plant, enhancing nutrient absorption and stress resistance. Moreover, glomalin can contribute to reducing CO_2 and N_2O, as it constitutes an important C and N reserve, suggesting that the inoculation with AMF in agricultural production systems can contribute to mitigate the effects of climate change (Rillig *et al.*, 2001).

Recently, Alptekin *et al.* (2025) reexamined the molecular nature of glomalin and observed a more positive immunological response, when using the monoclonal antigen Mab32B11, to an unidentified polysaccharide than to the commonly considered glycoprotein. Therefore, they suggested renaming glomalin to glomalose. Interestingly, the extraction method (as used in the present research) and functional attributes of glomalin are similar to those of glomalose.

This study highlights that inoculating strawberry plants with AMF benefits plant growth and physiology. However, future research is needed to explore interactions between different AMF and strawberry cultivars, as well as different substrates. It is also necessary to analyze the mechanisms involved in glomalin (glomalose) production, not only in the root but also in the soil, as well as the effects on moisture retention, to increase these benefits. This protein (carbohidrate) contributes to the formation and stabilization of aggregates in the soil due to its recalcitrance and hydrophobic nature (Wright and Anderson, 2000). In the present study, glomalin (glomalose) may play a similar effect to that of soil in substrates, decreasing water expenditure in plants inoculated with *F. mosseae* Mich. However, this aspect requires further investigation.

Principal Component Analysis

Figure 3 (A) shows that, for substrate 1, the first two components explain 79.2% of the total variability (66.7% and 12.5% for components 1 and 2, respectively). In substrate 2, these components explained 66.0% and 12.3% of the total variability, respectively (Figure 3 B). The PCA allowed us to identify the influence of substrates and treatments in obtaining

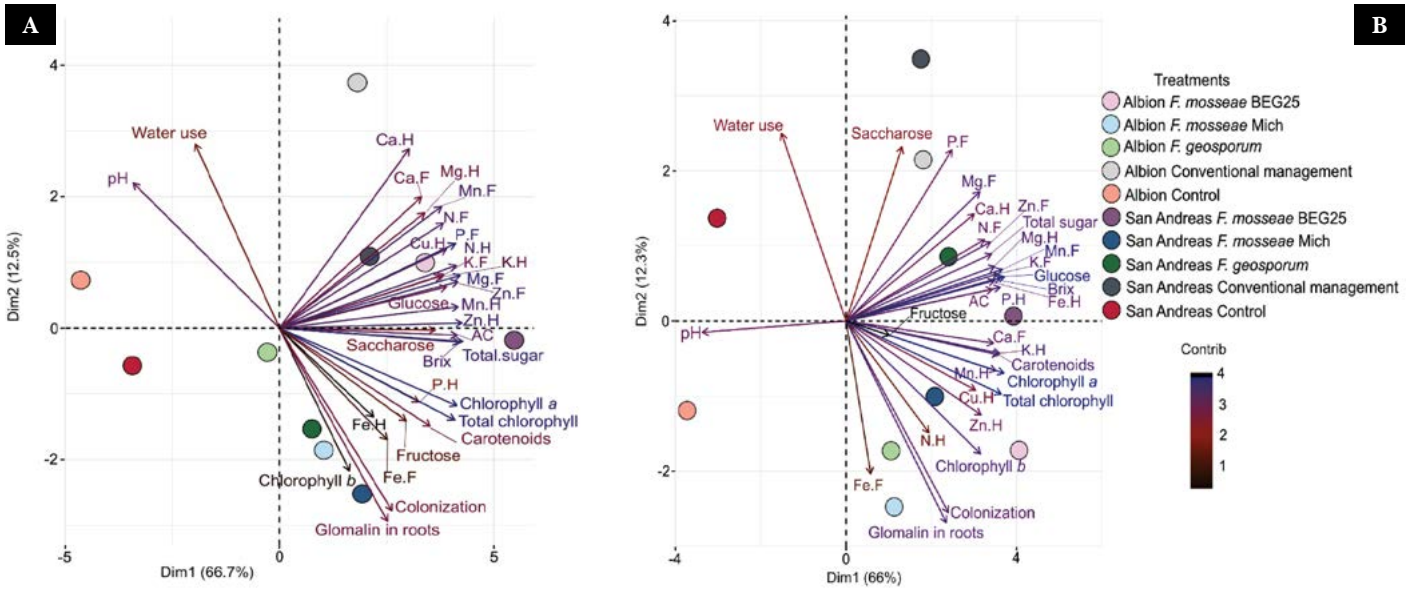

Figure 3. Principal component analysis of two strawberry cultivars (Albion and San Andreas) grown in substrate 1 (A) and substrate 2 (B) towards mycorrhiza inoculation.
FeF=iron in fruit, MnF=manganese in fruit, ZnF=zinc in fruit, CaF=calcium in fruit, MgF=magnesium in fruit, PF=phosphorus in fruit, KF=potassium in fruit, NF=nitrogen in fruit, CuL=copper in leaves, MnL=manganese in leaves, FeL=iron in leaves, ZnL=zinc in leaves, MgL=magnesium in leaves, CaL=calcium in leaves, KL=potassium in leaves, PL=phosphorus in leaves, NL=nitrogen in leaves, Brix=Brix degrees, pH=pH of the fruit, AC=titratable acidity in fruit

plants or fruits with specific, more desirable characteristics. The main trends that occurred in both substrates were as follows: 1) In substrate 1, no variable (vector) was associated with the control treatment. In contrast, different vectors were associated with the AMF-inoculated treatments and the M. conv treatment.

In substrate 2, the control treatments in both cultivars were associated with the pH vector, corroborating that fruits from control plants were less acidic.

2) In substrate 1, plants of both cultivars inoculated with *F. mosseae* Mich, as well as those of cultivar San Andreas inoculated with *F. geosporum* were associated with TGR, chlorophyll b, and percentage of colonization.

Notably, the vectors for TGR and percent colonization were oriented in the opposite direction to those for water use and pH. This suggests that higher TGR concentration and colonization percentage contribute to lower water expenditure, favoring fruit acidification in those treatments. In substrate 2, in the Albion cultivar, inoculation of plants with *F. mosseae* Mich and *F. geosporum* were also positively related to TGR and colonization but negatively related to water use.

3) In substrate 1, plants of the San Andreas cultivar inoculated with *F. mosseae* BEG25 showed a positive association with the fruit vectors of total sugar, sucrose, and °Brix. In substrate 2, plants of the cultivar San Andreas inoculated with *F. mosseae* BEG25 showed a positive relation with glucose and °Brix in the fruit. Conversely, plants treated with M. conv were only related to sucrose concentration in the fruit. This suggests that these treatments produced sweeter fruits, a characteristic preferred by consumers (Fan *et al.*, 2021). 4) In substrate 1, plants of the Albion cultivar inoculated with *F. mosseae* BEG25, as well as

those of the San Andreas cultivar with M. conv were positively associated with nutrient vectors in fruit (Ca, Mn, N, P, K, and Mg) and leaves (Mg, Cu, and K). In substrate 2, plants of cultivar Albion inoculated with *F. mosseae* BEG25, as well as those of San Andreas cultivar inoculated with *F. mosseae* Mich were positively associated with chlorophyll *b* concentration and leaf nutrients (N, Zn, and Cu). Those inoculated with *F. geosporum* were positively associated to nutrients in fruit (Mg, N, Zn, Mn, and K) and leaf (Ca, Mg, and P). Higher nutrient content in strawberry fruits benefits both producers and consumers. While producers improve crop nutrition for optimal production (Trejo-Téllez and Gómez-Merino, 2014), consumers value nutrient-rich fruits that fulfill specific bodily functions (Yahia *et al*., 2017).

CONCLUSION

Inoculation of strawberry plants with *F. mosseae* Mich was the most effective in reducing water use in both cultivars and substrates during the six-month evaluation period. This evidences its potential as a viable alternative for improving water-use efficiency in agriculture under climate change conditions. The reduction in water use is particularly relevant given the pressure that agriculture exerts on water resources and the declining availability of high-quality water. The PCA showed that mycorrhizal colonization and TGR were negatively associated with plant water use and varied according to cultivar, mycorrhizal fungus, and substrate. Compared to the M. conv treatment, plants inoculated with *F. mosseae* BEG25 yielded no differences under reduced fertilization conditions (which were used to avoid inhibiting AMF root colonization and to evaluate fungal effectiveness), mainly in nutrient uptake in the leaf (N, P, K, Ca, Mg and K, Cu, Mn and Zn) and fruit (N, P, K, Ca, Mg, Mn and Zn). This represents fertilizer savings of up to US$461 (per ha) in the production of greenhouse-grown strawberries. The inoculation also enhanced fruit nutrient concentration, Brix degrees, total sugar and glucose concentrations, and the percentage of citric acid, all parameters related to flavor and consumer preference. Therefore, AMF inoculation contributes to physiological, economic, and ecological benefits and should be implemented in the production of strawberry plants. Further research is needed to evaluate other substrates and more efficient irrigation methods. In addition, the assessment of fungal consortia used in this study or other AMF is required to understand their compatibility, effects on water use efficiency as well as the nutritional and nutraceutical quality of strawberry fruits, particularly under increasingly extreme climatic scenarios.

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