Mychorrhizal Fungi Inoculation Improves *Capparis spinosa*’s Yield, Nutrient Uptake and Photosynthetic Efficiency under Water Deficit

Mohammed Bouskout 1, Mohammed Bourhia 1, Mohamed Najib Al Feddy 2, Hanane Dounas 1, Ahmad Mohammad Salamatullah 3, Walid Soufan 4, Hiba-Allah Nafidi 5 and Lahcen Ouahmane 1,*

Abstract: Agricultural yields are under constant jeopardy as climate change and abiotic pressures spread worldwide. Using rhizospheric microbes as biostimulants/biofertilizers is one of the best ways to improve agro-agriculture in the face of these things. The purpose of this experiment was to investigate whether a native arbuscular mycorrhizal fungi inoculum (AMF-complex) might improve caper (*Capparis spinosa*) seedlings’ nutritional status, their morphological/growth performance and photosynthetic efficiency under water-deficit stress (WDS). Thus, caper plantlets inoculated with or without an AMF complex (+AMF and −AMF, respectively) were grown under three gradually increasing WDS regimes, i.e., 75, 50 and 25% of field capacity (FC). Overall, measurements of morphological traits, biomass production and nutrient uptake (particularly P, K\(^{2+}\), Mg\(^{2+}\), Fe\(^{2+}\) and Zn\(^{2+}\)) showed that mycorrhizal fungi inoculation increased these variables significantly, notably in moderate and severe WDS conditions. The increased WDS levels reduced the photochemical efficiency indices (Fe/Fm and Fo/Fo) in −AMF plants, while AMF-complex application significantly augmented these parameters. Furthermore, the photosynthetic pigments content was substantially higher in +AMF seedlings than −AMF controls at all the WDS levels. Favorably, at 25% FC, AMF-colonized plants produce approximately twice as many carotenoids as non-colonized ones. In conclusion, AMF inoculation seems to be a powerful eco-engineering strategy for improving the caper seedling growth rate and drought tolerance in harsh environments.

Keywords: abiotic stresses; *Capparis spinosa*; biostimulants; mycorrhizal inoculum; water-deficit stress; nutritional status; photochemical efficiency (Fe/Fm); photosynthetic pigments

1. Introduction

Caper-bush (*Capparis spinosa* L.), an orphan/indigenous medicinal and aromatic crop, is suited to the Mediterranean’s semi-arid and desert environments and is cultivated commonly by resource-constrained farmers. During dry seasons, caper cultivation provides a revenue stream for numerous farmers, compensating for yield losses from cereals and other crops. Morocco, Turkey, Italy and Spain are the world’s leading producers of capers (unopened immature flower buds) as well as caperberries (unripe fruit) [1,2]. It is a
perennial spiny shrub with many branches that belongs to the Capparaceae or Cappari-
daceae family and the genus *Capparis*, which has around 350 species [3]. This species
plays significant ecological and socio-economic functions, while also possessing important
therapeutic virtues. Caper parts are rich in bioantioxidants, making them an excellent
source of developing novel bioactive compounds with potent phytochemical and biological
benefits [4]. They might also be used as a substitute for synthetic preservatives in food
and pharmaceuticals/cosmetics products [5,6]. In addition to these very important and
attractive potential nutrapharmaceuticals, *C. spinosa* plants may play a wide variety of eco-
logical and environmental roles thanks to their xerophytic features. Indeed, the caper bush
cultivation has always been valuable owing to its well-deserved reputation for growing in
challenging conditions and on rough land, as well as agronomic characteristics associated
with drought resistance and high-temperature tolerance. This makes it a good candidate
for reclaiming land that does not have a lot of farming potential (marginal lands) [7]. In
the field conditions, there exist different works conducted in order to comprehend the
practical/advantageous strategies and mechanisms of caper tissue adaptation in response
to drought stress. This xerophytic plant’s anatomical, morphological, physio-biochemical
adaptations and survival strategies have been well described, allowing it to grow and
successfully complete its life cycles in arid–semi-arid environments [3,8–14]. Additionally,
a transcriptome investigation of this xerophytic plant also indicates a molecular basis frame-
work for its abiotic-stress resistance, hence the plant’s molecular plausible explanation for
its ability to thrive in the desert [15].

In fact, as global warming continues to rise, the likelihood of extreme occurrences such
as an extended duration and the greater intensity/severity of drought increases as well.
This context projection is more likely to occur in the desert or semi-arid regions of the world,
particularly in Eastern Asia, Africa and the Mediterranean basin, which represents the
distribution and intensification area of *C. spinosa* [15]. Water scarcity, lack of rain and rising
temperatures resulting from climate change render the earth drier. Increasing dryness
is becoming a worldwide trend that is negatively influencing both socio-economic and
agro-ecosystem aspects. The plants’ growth and yield of different crops are often affected
by drought and nutritional disruptions such as environmental restrictions, which provide
a growing global hazard that the COVID-19 pandemic conjecture eclipses today [16].
Droughts disturb the water balance and cause toxicity by altering ionic homeostasis, hence
diminishing plant productivity. In this respect, environmental deterioration caused by
protracted droughts, excessive soil erosion and poor soils productivity would limit the
caper species’ ability to reach its optimal growth/yield and intensification potential. Earlier
studies that looked at how abiotic stressors such as salt and drought affect *Capparis spinosa*
seedlings found that growth and other qualities are considerably lower when there is not
enough water. Plant height, leaf number, leaf length, both shoot fresh and dry weights
and chlorophyll, as well as the relative content of leaf and root, were all significantly
lower when water-deficit stress (WDS) increased [17,18]. Additionally, substantial losses in
yield per hectare and water use efficiency were seen when WDS was imposed at various
irrigation intervals. The carotenoids content and electrolyte leaks were also affected, and the
detrimental effect of WDS contexts was compensated using a superabsorbent polymer [19].

On the other hand, inoculation with two arbuscular mycorrhizal fungi species (AMF)
promoted the growth and biomass of *Capparis spinosa* plants, its nutrient uptake (phosphate
and nitrogen), and stimulated various biochemical and physiological traits [20]. According
to Pugnaire and Esteban [21], phosphate and nitrogen fertilizers improve caper bush growth
and the content of all the mineral nutrients in plant tissues; they also hypothesize that caper
plants may flourish in nutrient-poor soils thanks to their extensive mycorrhizal root system.
In fact, mycorrhizal fungi are a kind of ubiquitous rhizospheric soil microorganism that
may establish symbiotic relationships with plant roots and govern plant development [22].
Interestingly, AMF have been proven to be one of the wonderful keys to optimizing
most plant crop traits under diverse environmental stresses [23–33]. Thus, biotechnology
approaches might be effective in strengthening caper production and intensification in
degraded habitats, as well as in attempting to unlock the full potential of this species to promote sustainable agriculture and accomplish the abovementioned ecological and socioeconomic advantages. AMF application may be a means of ensuring the sustained efficiency of commercial caper crops. Accordingly, to the best of our knowledge, no published research has looked into the effect of mycorrhizal fungi on the physiological and morphological performance of *C. spinosa* plants under water-deficit stress conditions. For these purposes, this study focused on *C. spinosa* and its associated microbiota, the native AMF complex in particular, to explore whether there was a potentially beneficial symbiotic association in improving the biomass production and nutritional status of mycorrhized seedlings, as well as their photosynthetic performance, under progressively reduced soil moisture levels to impose drought stress.

2. Materials and Methods

2.1. Plant Material

The caperberries (fruit) of capers (*Capparis spinosa* L.) were reaped from the Safi region of Morocco (32°12′12.0″ N; 9°09′04.6″ W) in July 2017. The seeds were then separated from the ripe fruit, cleaned in tap water, dried and stored in linen sacks at room temperature before they were sown. The seeds were chemically treated with a mix of sulfuric and gibberellic acid (H$_2$SO$_4$ and GA$_3$) at the time of germination to break the dormancy they suffered. Subsequently, the seeds were disinfected with 3% sodium hypochlorite for 10 min, accompanied by three distilled water rinses [34]. They were put in Petri dishes (9 cm Ø) onto paper soaked in distilled water and incubated at 25 °C. The filter papers were replaced at frequent intervals to avoid contamination from yeasts. Pre-germinated seeds were then transferred into small polystyrene plastic containers full of sterilized black peat. They were transplanted again to other polystyrene pots (2 L) when young seedlings had four to five fully formed leaves.

2.2. Rhizospheric Soil Samples

Sandy loam soil was collected from two caper fields in the Safi area of Morocco at a depth of approximately 32–45 cm under mature and very well growing plants of *C. spinosa*. The soil samples were taken from the same seeds sampling site. The sieved (≤2 mm) and homogenized rhizospheric soil samples had 16.6 ± 1.06 (mS m$^{-1}$) of electrical conductivity EC, 8.16 ± 0.09 of pH (H$_2$O), 19.5 ± 2.72 (%) total carbonates (CaCO$_3$), 2.16 ± 0.1 (%) of total organic carbon, 3.72 ± 0.15 (%) if organic matter, 1.83 ± 0.21 (mg g$^{-1}$) of P-Olsen and 2.61 ± 0.14 (mg g$^{-1}$) of total P. The soil texture consisted of 67.3% sand, 23.1% silt and 9.6% clay. In this experimentation, the physicochemically characterized rhizospheric soil samples were used as one-half of the substrate for cultivating each caper plantlet.

2.3. Mycorrhizal Fungi Inoculum

The mycorrhizal fungi inoculum (MFI) was made up of a mixture of indigenous arbuscular mycorrhizal fungi spores (AMF complex) gained in rhizospheric soil samples taken underneath mature caper plants (*Capparis spinosa*) in Morocco’s Safi region. In this experiment, the trap culture technique was used [35]. The native AMF complex was propagated for 12 weeks on the maize roots (*Zea mays* L.) as a mycotrophic plant species. This trap culture was applied to amplify and enrich the amount of indigenous AMF complex associated with wild caper plants. Parallel to, prior to and after that, a preliminary examination of AMF spores complex at morphotype scale was conducted using a specific key [36] to monitor their quantitative and qualitative presence as well as their survival in abundance. Wet sieving (mesh 500 to 45 µm) 100 g of dry soil followed by the centrifugation (1500 rpm for 10 min) of the spores trapped in aqueous sucrose solution (50% w/v) resulted in the extraction of AMF spores from rhizospheric soil samples, as described by Ouahmane et al. [35]. With the use of a stereomicroscope, AMF spores were enumerated such that the prepared AMF inoculum contained ~615 ± 38 spores/100 g of trap culture assemblage. MFI
mainly includes mycorrhizal spores, infected trap root segments and viable mycorrhizal hyphae that serve as active AM fungal propagules.

2.4. Experimental Design and Treatments

The experiment was set up as a two-factor interaction with a complete randomization (i.e., the inoculum of native AMF complex and water stress treatments). Ten replicates were performed for each treatment, giving sixty pots in total. Inoculated seedlings were cultivated on a substrate made of a mixture (1.5 kg) of sterilized river sand and sterilized sampled rhizospheric soil (1:1, v/v), as well as 5 g of freshly prepared MFI. The mycorrhizal inoculum was placed near each seedling root to maximize fungal colonization. The uninoculated plants (control) were grown in the same homogeneous substrate sterilized three times at 180 °C. Then, three-month-old healthy plantlets of the caper were randomly subjected to one of three irrigation water treatments. The gravimetric technique was employed to measure the soil field capacities applied in pots. At first, all dry pots were weighed (w1) and well-watered to saturate the substrate thoroughly, then weighed again (w2) when excess water had drained (after ~48 h). The difference between the two weights (w3 = w2 − w1) was used for achieving 75, 50 and 25% FC levels. All pots were adjusted twice daily at twelve-hour intervals. Cumulative water loss was supplemented to all pots every day during the experimental period to compensate for natural transpiration/soil evaporation and leaching/percolation processes, thus maintaining soil moisture conditions for each targeted FC level. The seedlings were grown in a sunny greenhouse under natural daylight. The temperature ranged from ~22 to ~38.1 °C throughout the experiment, with a relative humidity of ~60–70% and a photoperiod of approximately 12 h.

2.5. Growth Measurements

After twelve weeks of cultivation, the morphological traits and biomass characteristics of mycorrhizal (+AMF) and non-mycorrhizal (−AMF) caper plantlets were recorded during and after harvesting. Firstly, the height of seedlings was measured, as well as the number of leaves, nodes and branches on each shoot. The collar diameter was measured with the aid of a digital Vernier caliper. Afterward, all plantlets were gently withdrawn from the soils, and the shoot parts of ten randomly selected uprooted seedlings were carefully separated from their root systems. Following that, the fresh weights of shoots and roots were determined using an electronic precision balance (~0.001 g). At the same time, after all the samples were deposited for 24 h in a dry oven at 110 °C, their dry weights were estimated. The root-to-shoot (Rdw/Sdw) ratio index was then calculated for each plant sample by dividing root dry weight by shoot dry weight. The relative biomass allocation to roots was determined using the root weight ratio (RWR) parameter as total root dry weight (g) divided by total plant dry weight (g). The mycorrhizal dependency (MD%), which is the MFI’s contribution to seedlings growth, was calculated using the total dry weight (dry wt.) ratio of +AMF and −AMF caper plantlets as follows:

$$\text{MD} \% = \left( \frac{\text{Total dry wt.of } + \text{AMF plantlets} - \text{Total dry wt. of } - \text{AMF plantlets}}{\text{Total dry wt.of } + \text{AMF plantlets}} \right) \times 100$$  \hspace{1cm} (1)

The average values of morphological and biomass parameters of all plants were obtained using six replicates.

2.6. Plant Mineral Analysis

An aliquot of 500 mg of the aerial plant samples was dried (80 °C/24 h), calcined (at 550 °C/5 h) and digested by a freshly prepared mix diacid of 65% HNO3 and 37% HCl (1:3, v:v), respectively. By way of Whatman paper (no. 42), the resulting digested dry matter solutions were purified and then diluted to 50 mL with deionized water. The content of macronutrients (phosphorus, potassium, magnesium, sodium and calcium) and micronutrients (iron and zinc) of all samples were measured using an ICP-AES (ICPE-9000,
Nutrient content values were expressed as mg g\(^{-1}\). The average content of all macro- and micronutrients was determined using five replicates.

2.7. Chlorophyll Fluorescence

In vivo, special clips were mounted on the young leaves of five individual plantlets of each treatment to be adapted to the dark for 30 min between 10:00 and 12:30 a.m. After the excitation of the leaves with high-intensity actinic light for 0.1 s, the parameters of leaf chlorophyll fluorescence, especially \(F_o\), \(F_v\) and \(F_m\) reflecting minimum, variable and maximum fluorescence yields, respectively, were determined automatically using a handheld chlorophyll fluorometer OS-30p\(^+\) (Opti-Sciences, Hudson, NY, USA). The calculated \(F_v/F_m\) ratio \((F_m - F_o)/F_m\) represents the maximum quantum efficiency-(yield) of open photosystem II (PSII) centers. The \(F_v/F_o\) ratio changes, describing the basal quantum yield (maximum primary yield of PSII photochemistry), were also studied. The average values of each chlorophyll fluorescence parameter were determined using five biological replicates.

2.8. Content of Photosynthetic Pigments

Fresh leaves (~50 mg) were homogenized into 3 mL of ice-cold acetone (100%) for each sample. The extract was centrifuged for 10 min at 1000 rpm and incubated in the dark at 4 °C for 12 h. The collected supernatant was measured spectrophotometrically at 662, 645 and 470 nm for chlorophyll a (Chl \(a\)), chlorophyll b (Chl \(b\)) and total carotenoids (Cart), respectively. The calculation formulas of Lichtenthaler [38] were used and the results were expressed in mg pigment concentrations per gram of fresh leaf (mg g\(^{-1}\) FW). Six samples were analyzed to measure the mean amounts of every chlorophyll pigment parameter.

2.9. Symbiotic Development

For each mycorrhizal treatment (n = 3), very fine fresh roots were cleared with 10% (w/v) KOH (2.5 h at 90 °C) before being neutralized with a 5% solution of HCl. They were then stained at 90 °C for 30 min with trypan blue 0.05% (w/v) in lactoglycerol solution. After each step, each sample was adequately rinsed with distilled water to eliminate all traces of KOH, HCl and excess trypan blue [39]. Colored root fragments of 1 cm were mounted parallel on a microscope slide. The degree of mycorrhizal caper root colonization was then estimated according to the method defined by Trouvelot et al. [40] below a microscope at 40-X magnification. A sample (n = 3) of uninoculated roots (plantlets grown without AMF) was examined randomly to ensure favorable experimental conditions.

2.10. Statistical Analysis

All parameters were expressed as mean values ± standard deviations (SD). A two-way analysis of variance (2-way ANOVA) was conducted in order to determine if inoculation with AMF-complex (A) and soil WDS (W) levels had a statistically significant influence on all variables examined in caper plants, separately and/or in combination. All the data were first checked for normality (Shapiro–Wilk test) and homoscedasticity (Levene test) to ensure the conditions of the parametric ANOVA test. Tukey’s post hoc test subjected the averages of all parameters to multiple comparisons if the two factors (A × W) interacted significantly. Whenever \(p < 0.05\), a difference was deemed to be statistically significant. Furthermore, the gathered data were examined using the correlation approach, which included the factorial analysis method with principal component extraction (PCA) and correlation analysis using the Pearson’ \(r\) coefficient to perceive different links among all studied variables and within factor treatments. The statistical analysis was conducted with the IBM SPSS version 23.0 package, and the graphs were made with GraphPad Prism 9 software.
3. Results
3.1. Mycorrhizal Colonization

The mycorrhizal infection of caper plantlet roots by the native AMF complex was effective, as highlighted by the mycorrhizal colonization (MC) frequency parameter (Figure 1). The lowest MC rates were registered in well-watered seedling roots (41.7%), which were found to be statistically different from those grown in moderate (55.3%) and extreme (51.7%) WDS conditions. The MC frequency first went up by ~32.6% with the rise in WDS levels from 75 to 50% FC and then started declining by ~6.5% after diminishing further field capacity from 50 to 25%. In contrast, no mycorrhizal colonization was found in the uninoculated plant roots under all the water regimes. The mycorrhizal dependency (MD) results, as a rate (%) indicator of the improvement in the total dry biomass of the caper plants in response to the AMF complex inoculation, followed the same variation trend as MC across different WDS treatments (Figure 1). MD rose significantly from 29.5% in well-watered conditions (75% FC) to 56.1% under moderate WDS (50% FC), then diminished insignificantly by 33.9% to attain 37% at severe WDS (25% FC).

![Figure 1](image-url)

**Figure 1.** Mycorrhizal colonization rate (MC (%), white bars) and mycorrhizal dependency (MD (%), grey bars) of *C. spinosa* +AMF seedlings at three levels of water-deficit conditions (D1—75%, D2—50% and D3—25% FC). The bar chart with error bars represents the means and SD of three replicates. Asterisks indicate significant differences between water-deficit stress treatments (α = 0.05), as determined using one-way ANOVA, followed by post hoc Tukey’s tests (*, p < 0.05).

3.2. Morphological Parameters

Table 1 displays the morphological traits measured after harvesting the mycorrhizal and non-mycorrhizal (−AMF) seedlings of *C. spinosa* that underwent three separate irrigation regimes (75, 50 and 25% of FC). Overall, the inoculated plantlets’ morphological characteristics at all irrigation levels were significantly better than those grown without the AMF complex (p < 0.0001). By comparison, the WDS factor, alone or in combination with the AMF treatment, did not influence all the morphological parameters statistically significantly. The elevated irrigation levels led to a gradual augmentation in stem elongation (maximum plant height) for both the mycorrhizal and −AMF plantlets; simultaneously, the WDS conditions have not affected this parameter seriously (p = 0.06), whereas the AMF complex treatment improved the caper plant height at all the FC levels. In all the watering conditions, the nodes number and thus the number of leaves under the presence of MFI were significantly very superior to those of uninoculated seedlings, becoming greater by ~172%/~117% and ~118%/~113%, respectively, at 50%/25% FC for both leaves and nodes number. In the absence of the AMF complex, the branches number decreased approximately two-fold at 75% FC and more than fourfold at 50% and 25% field capacity. The collar
diameter of +AMF plants was considerably more vigorous than those of uninoculated seedlings at all the WDS levels, improving by ~18.04, ~25.13 and ~26.82 at 75, 50 and 25% FC, respectively.

Table 1. Morphological traits of C. spinosa seedlings grown without (−AMF) or with (+AMF) mycorrhizal fungi inoculum under three water stress levels (% FC).

| Water Stress (% FC) | Mycorrhizal Inoculation | Plant Height (cm plant⁻¹) | Leaves (no. plant⁻¹) | Branches (no. plant⁻¹) | Nodes (no. plant⁻¹) | Collar Diameter (mm plant⁻¹) |
|---------------------|-------------------------|----------------------------|----------------------|------------------------|---------------------|-------------------------------|
| 75% FC              | − AMF                   | 14.9 ± 0.7 b               | 21 ± 2.0 b           | 3 ± 1.0 b              | 31.7 ± 5.0 b        | 5.4 ± 0.4 bc                  |
|                     | + AMF                   | 24.2 ± 0.3 a               | 43 ± 5.0 a           | 6 ± 0.0 a              | 52.3 ± 5.1 a        | 6.4 ± 0.7 bc                  |
| 50% FC              | − AMF                   | 13.7 ± 1.6 b               | 18 ± 1.0 b           | 1.3 ± 0.6 b            | 25 ± 3.0 b          | 5.6 ± 0.4 bc                  |
|                     | + AMF                   | 22.7 ± 2.4 a               | 49 ± 12.4 a          | 6.3 ± 1.5 a            | 58.7 ± 7.5 a        | 7.0 ± 0.01 a                  |
| 25% FC              | − AMF                   | 13.4 ± 1.2 b               | 21.7 ± 1.5 b         | 1.3 ± 0.6 b            | 27 ± 1.0 b          | 5.1 ± 0.1 c                   |
|                     | + AMF                   | 21.4 ± 0.6 a               | 47.3 ± 7.2 a         | 5.7 ± 0.6 a            | 53.3 ± 12.5 a       | 6.4 ± 0.7 ab                  |

Water stress (W) | ns | ns | ns | ns | ns | ns
AMF inoculation (A) | **** | **** | **** | **** | *** | ns
W × A | ns | ns | ns | ns | ns | ns

Values are means ± SD (n = 6). The means of each morphological parameter in a single column followed by a similar letter, between both mycorrhizal and non-mycorrhizal plantlets at all levels of water-deficit conditions, are not significantly different according to Tukey’s post hoc test; Asterisks denote the significance levels of the effect of AMF (A), water-deficit (W) and their interaction (A × W) on each parameter measured, based on the 2-way ANOVA test: (***, p < 0.001; ****, p < 0.0001 and ns, no significance p > 0.05).

3.3. Biomass Production

The mycorrhizal plants’ shoot fresh and dry weights (SFW and SDW) decrease marginally as the field capacity declines, unlike the AMF-untreated plantlets, their SFW and SDW decrease significantly (p < 0.001) once the levels of soil moisture decrease (Table 2). On the other side, as the WDS increases in mycorrhizal C. spinosa seedlings, the root fresh and dry weights (RFW and RDW) significantly boost (p < 0.001), with a slight rise but one that is not significant in −AMF plants. As a reaction to the dwindling soil moisture, the substantial increase in the RFW and the RDW in the mycorrhizal plants thus contributes to greater total fresh and dry weights (TFW and TDW). In contrast, −AMF seedlings maintain almost the same TFW and TDW under all the conditions of WDS. The maximum improvements in the RFW (13.88 g), RDW (4.33 g), TFW (19.40 g) and TDW (5.84 g) were obtained at 50% FC in the +AMF plants. All the biomass parameters of the −AMF plantlets, whatever the WDS level, were all significantly lower than those of the mycorrhizal seedlings (except the RDW at 75%) (p < 0.0001). In the absence of an AMF mixture at moderate and extreme WDS, the caper plants’ SFW fall markedly by approximately 105–64%, the SDW by 137–83%, the RFW by 135–76%, the RDW by 125–50% and then the TFW and TDW by 125–128% and 72–58%, respectively. Moreover, the root-to-shoot (R_{dw}/S_{dw}) ratio and the root weight ratio (RWR) were similar for both the +AMF and −AMF plants at all watering regimes. However, when the soil moisture was lower, these two parameters increased significantly. The water-deficit conditions greatly influenced all the biomass parameters (apart from TFW, p = 0.08), all of which were significantly positively affected by the AMF treatment alone (p < 0.0001) or in interaction with the WDS treatments (except R_{dw}/S_{dw} and RWR) (Table 2).
Table 2. Shoot fresh and dry weights (SFW and SDW), root fresh and dry weights (RFW and RDW), total fresh and dry biomass (TFW and TDW), root-shoot ratio (R_{dw/S_{dw}}) and root weight ratio (RWR) of non-mycorrhizal (−AMF) and (+AMF) mycorrhizal C. spinosa plantlets at three levels of water-deficit stress (% FC).

| Water Stress (% FC) | Mycorrhizal Inoculation | SFW (g plant\(^{-1}\)) | RFW (g plant\(^{-1}\)) | SDW (g plant\(^{-1}\)) | R_{dw/S_{dw}} | RWR |
|---------------------|------------------------|-----------------------|-----------------------|-----------------------|--------------|------|
| 75% FC              | −AMF                   | 4.3 ± 0.3\(^a\)       | 6.2 ± 0.8\(^c\)       | 1.0 ± 0.2\(^bc\)     | 1.6 ± 0.3\(^c\) | 10.4 ± 0.8\(^c\) |
|                     | +AMF                   | 5.6 ± 0.4\(^a\)       | 9.6 ± 1.1\(^b\)       | 1.5 ± 0.1\(^a\)      | 2.1 ± 0.2\(^c\) | 15.2 ± 1.3\(^b\) |
| 50% FC              | −AMF                   | 2.7 ± 0.3\(^c\)       | 5.90 ± 0.4\(^e\)      | 0.6 ± 0.1\(^c\)      | 1.9 ± 0.4\(^c\) | 8.6 ± 0.1\(^c\) |
|                     | +AMF                   | 5.5 ± 0.2\(^a\)       | 13.9 ± 0.6\(^a\)      | 1.5 ± 0.3\(^a\)      | 4.3 ± 0.4\(^a\) | 19.4 ± 0.7\(^a\) |
| 25% FC              | −AMF                   | 3.1 ± 0.1\(^c\)       | 6.9 ± 0.7\(^c\)       | 0.7 ± 0.1\(^c\)      | 2.1 ± 0.3\(^c\) | 10.0 ± 0.8\(^c\) |
|                     | +AMF                   | 5.1 ± 0.1\(^a\)       | 12.2 ± 0.9\(^a\)      | 1.3 ± 0.2\(^ab\)     | 3.2 ± 0.2\(^b\) | 17.3 ± 1.0\(^b\) |

Means ± SD are the values of n = 6 replicates. According to Tukey’s post hoc test, means of each parameter followed by distinct letters in the same column, for +AMF and −AMF plantlets between all levels of water-deficit conditions, are significantly different; Asterisks denote the significance levels of the effect of AMF (A), water-stress (W) and their interaction (A × W) on each parameter measured, based on the 2-way ANOVA test: (*, p < 0.05; **, p < 0.01; *** p < 0.001; ****, p < 0.0001 and ns, no-significance).

3.4. Macro- and Micromineral Nutrient Contents

Table 3 data illustrate how much the inoculation with a mixture of native AMF has improved the mineral uptake in droughted caper plantlets compared to −AMF ones. Overall, the mycorrhizal C. spinosa seedlings recorded the highest mineral contents at all soil moisture levels. The two-way ANOVA revealed that, apart from sodium (Na\(^+\)) and calcium (Ca\(^2+\)) (p > 0.05), the native AMF complex had a statistically positive significant effect on the variation of plantlet mineral nutrients, i.e., phosphorus (P), potassium (K\(^+\)), magnesium (Mg\(^2+\)), iron (Fe\(^2+\)) (p < 0.0001) and zinc (Zn\(^2+\)) (p < 0.01). Additionally, except for P (p < 0.001) and Fe\(^2+\) (p < 0.05), the WDS levels did not significantly affect the other mineral nutrients measured in caper shoots. By contrast, neither the AMF treatment (A) nor WDS conditions (W) nor their interaction (A × W) greatly affected the Na\(^+\) and Ca\(^2+\) amounts in the caper shoots. Only the P and Fe\(^2+\) concentrations were appreciably influenced by the interaction between the AMF inoculation and the soil moisture deficit conditions among the macro and micro-minerals examined. At 75, 50 and 25% of field capacity, the shoot P is ~44, ~52% and ~69% higher in the inoculated seedlings than in their counterparts grown in soil without the native AMF complex, respectively; similarly, K\(^+\) was elevated by ~45–40%, Mg\(^2+\) by ~45–55% and Zn\(^2+\) by ~53–66% at 50% and 25% FC, respectively, and the Fe\(^2+\) concentration increased approximately twice as the WDS increased.

3.5. Chlorophyll Fluorescence

The observed mean minimal (F\(_0\)), variable (F\(_v\)) and maximal (F\(_m\)) fluorescence values did not significantly differ at any water-deficit stress level in inoculated and non-inoculated C. spinosa dark-adapted leaf. In comparison to the −AMF seedlings (control), the AMF inoculation leads to a substantial increase (p < 0.05) in the mean PSII photochemical (F\(_v/F\(_m\)) maximum quantum efficiency ratio as well as the basal quantum efficiency (F\(_0/F\(_m\)) at both mild and extreme WDS conditions. The youngest C. spinosa leaves had a lower F\(_0\) but a higher F\(_v\) and F\(_m\) in the AMF-treated plantlets than in the control ones when the soil water deficit worsened. The water stress factor solely affected F\(_v\) and F\(_m\) (p < 0.05), whereas both F\(_v/F\(_m\) and F\(_0/F\(_m\) were considerably influenced by the AMF inoculation treatment alone or in combination with the WDS (p < 0.01) (Table 4).
Table 3. Mineral macro- and micronutrients content of *C. spinosa* shoots cultivated without (−AMF) or with (+AMF) AMF-complex at three advancing water-deficit levels (% FC).

| Treatments | Water Stress (% FC) | Mycorrhizal Inoculation | P (mg.g⁻¹) | K⁺ (mg.g⁻¹) | Na⁺ (mg.g⁻¹) | Ca²⁺ (mg.g⁻¹) | Mg²⁺ (mg.g⁻¹) | Fe²⁺ (mg.g⁻¹) | Zn²⁺ (mg.g⁻¹) |
|------------|---------------------|-------------------------|------------|-------------|-------------|--------------|--------------|--------------|-------------|
|            | 75% FC              | −AMF                    | 1.4 ± 0.1  | 15.1 ± 1.3  | 27.5 ± 1.3  | 11.6 ± 1.5  | 3.4 ± 0.7    | 0.8 ± 0.1    | 0.05 ± 0.02  |
|            |                     | +AMF                    | 2.0 ± 0.3  | 9.5 ± 0.9   | 29.5 ± 1.3  | 13.4 ± 2.0  | 4.6 ± 0.4    | 1.6 ± 0.1    | 0.07 ± 0.02  |
|            | 50% FC              | −AMF                    | 1.4 ± 0.1  | 11.3 ± 2.2  | 27.0 ± 3.4  | 12.1 ± 1.8  | 3.4 ± 0.4    | 0.9 ± 0.1    | 0.04 ± 0.01  |
|            |                     | +AMF                    | 2.1 ± 0.1  | 16.5 ± 1.4  | 28.3 ± 1.6  | 14.4 ± 2.3  | 4.9 ± 0.3    | 1.8 ± 0.1    | 0.07 ± 0.01  |
|            | 25% FC              | −AMF                    | 1.6 ± 0.1  | 11.8 ± 1.6  | 28.3 ± 1.6  | 13.9 ± 1.7  | 3.2 ± 0.2    | 0.9 ± 0.1    | 0.05 ± 0.01  |
|            |                     | +AMF                    | 2.7 ± 0.1  | 16.6 ± 1.9  | 30.9 ± 0.2  | 14.9 ± 0.6  | 4.9 ± 0.2    | 1.9 ± 0.1    | 0.08 ± 0.02  |

Water stress (W) and their interaction (A × W) on each parameter measured, based on the 2-way ANOVA test: (*, p < 0.05; **, p < 0.01; ***p < 0.001; ****, p < 0.0001 and ns, no-significance p > 0.05).

Table 4. Changes of chlorophyll fluorescence parameters in leaves of *C. spinosa* seedlings cultivated without (−AMF) or with (+AMF) AMF-complex under three irrigation levels (% FC) (Fo-initial fluorescence, Fv-variable fluorescence, Fm-maximum fluorescence, Fe/Fm-maximum quantum efficiency and Fe/Fo-basal quantum yield).

| Treatments | Water Stress (% FC) | Mycorrhizal Inoculation | Fo | Fv | Fm | Fe/Fm | Fe/Fo |
|------------|---------------------|-------------------------|----|----|----|-------|------|
|            | 75% FC              | −AMF                    | 34.7 ± 10 b | 119 ± 29.5 a | 153.7 ± 39 a | 0.78 ± 0.02 abc | 3.5 ± 0.3 ab |
|            |                     | +AMF                    | 43.7 ± 4.2 ab | 129.3 ± 5.9 a | 173 ± 9.5 a | 0.75 ± 0.01 abc | 3.0 ± 0.2 ab |
|            | 50% FC              | −AMF                    | 48 ± 7.9 a  | 132 ± 19.9 a | 180 ± 27.9 a | 0.73 ± 0.01 bc  | 2.8 ± 0.1 b  |
|            |                     | +AMF                    | 40.7 ± 2.1 ab | 162.3 ± 22 a | 203 ± 23.1 a | 0.80 ± 0.02 a   | 4.0 ± 0.6 a  |
|            | 25% FC              | −AMF                    | 56.7 ± 9.5 a | 147.7 ± 10 a | 204.3 ± 6.0 a | 0.72 ± 0.05 c   | 2.7 ± 0.6 b  |
|            |                     | +AMF                    | 42.3 ± 4.5 ab | 161 ± 14.2 a | 203.3 ± 18 a | 0.79 ± 0.01 ab  | 3.8 ± 0.2 a  |

Means of n = 5 replicates ± SD. Means of each parameter accompanied by distinct letters in one column, for mycorrhizal and non-mycorrhizal *C. spinosa* plantlets between all levels of water-deficit conditions, are significantly different according to Tukey’s post hoc test; Asterisks denote the significance levels of the effect of AMF (A), water-deficit (W) and their interaction (A × W) on each parameter measured, based on the 2-way ANOVA test: (*, p < 0.05; **, p < 0.01; ***p < 0.001; ****, p < 0.0001 and ns, no-significance p > 0.05).

3.6. Photosynthetic Pigments

Chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Chl a+b) and total carotenoids (Cart) were accumulated in both mycorrhizal and non-mycorrhizal *C. spinosa* seedlings when they were subjected to increasing water restrictions (Figure 2). All the photosynthetic pigment variables were considerably changed by the AMF-complex inoculation (A). The same goes for water-deficit conditions (W). In contrast, their interaction did not have a significant effect on the content of all the photosynthetic pigments. Moreover, the differences of the Chl a, Chl b and Chl a+b concentrations were significant between the AMF-inoculated and non-inoculated *C. spinosa* plantlets under all the irrigation levels, and just at 25% FC for Cart, based on Tukey’s post hoc test (at p < 0.05). Interestingly, the significance of the variations’ magnitude in Chl a+b concentrations between the +AMF and −AMF plantlets at all the levels of WDS is the same as that observed in Chl a, suggesting
that this photosynthetic pigment may govern the total chlorophyll content. The increase in soil moisture-deficit from 75 to 50% and then to 25% of the FC led to a significant increase in the concentration of Chl b in the mycorrhizal seedlings compared to the − AMF ones, which, under all the FC conditions, had no significant change in Chl b but doubled their content at 25% FC. The Chl a/b ratio increased in the absence of the AMF complex and decreased with the severe WDS. Still, statistically, the interaction impact of AMF-inoculation status and different WDS conditions was insignificant (p = 0.98). The Chl a, Chl b, Chl a+b and Cart concentrations in the +AMF caper seedlings were ~98, ~155, ~110 and ~38% greater than those in the −AMF plantlets at both corresponding soil moisture levels of 75 and 50% FC, respectively, while at 25% FC, they were ~40, ~92, ~54 and ~80% higher (Figure 2).

Figure 2. Chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Chl a+b), carotenoids (Cart) content and chlorophyll a/b ratio (Chl a/b) of C. spinosa seedlings’ fresh leaves cultivated without (AMF−, white bars) or with (AMF+, grey bars) native mycorrhizal fungi inoculum under three irrigation levels (% FC). The bars represent the mean ± SD of n = 6 replicates. Bars sharing a common lowercase letter reveal no significant difference according to Tukey’s post hoc test at p < 0.05. Asterisks denote the significance levels (P) of the effect of AMF (A), water-deficit (W) and their interaction (A × W) on each parameter measured, based on the 2-way ANOVA test: (**, p < 0.01; ***, p < 0.001; ****, p < 0.0001 and ns, no-significance p > 0.05).
3.7. Relationship between Caper Seedlings Traits

Figure 3 of Biplot, which focuses on the principal component analysis (PCA), depicts the variations of all the measured caper plant parameters allowing us to contemplate how interrelated the variables are to one another regarding each WDS level and AMF inoculation treatment. The first (PC1) and second (PC2) principal components clarify 60.39 and 14.20%, respectively, i.e., ~74.59% of the total variance. The PCA score plot clearly segregated all the AMF treatments along PC1, with mildly and extremely droughted mycorrhized caper plantlets positioned at the positive section of PC1 that is marked by the higher plantlets’ growth traits, and high levels of all the chlorophyll pigments, $F_v/F_m$, $F_o/F_v$, as well as all the mineral nutrients (Figure 3). RWR, $R_{\text{dw}}/S_{\text{dw}}$, $F_m$ and $F_o$, on the other hand, had the highest load in the second component, which visibly separates all the water stress levels, while $F_o$, $F_m$ and $Ca^{2+}$ align with both. However, Chlorophyll a/b aligns somewhat more with a negative section of PC1.

![Biplot of principal components analysis (PCA)](attachment:image.png)

**Figure 3.** Biplot of principal components analysis (PCA) based on all measured parameters of *C. spinosa* plantlets exposed to various levels of water-deficit conditions (75, 50 and 25% FC) and AMF treatment. The blue contour lines assign the variables, and the six colored forms-points symbolize all different treatment groups. Myc (%) = Mycorrhizal colonization rate, MD (%) = Mycorrhizal dependency, P-h = Plant height, L-n = Leaves no., B-n = Branches no., N-n = Nodes no., C-d = Collar-diameter, TFW = total fresh weight, TDW = Total dry weight, SFW = shoot fresh weight, SDW = Shoot dry weight, RFW = Root fresh weight, RDW = Root dry weight, $R/S$ = Root-to-shoot ratio, RWR = Root weight ratio, $K$ = Potassium, Mg = Magnesium, Fe = Iron, P = Phosphorus, Zn = Zinc, Na = Sodium, Ca = Calcium, Chl $a$ = Chlorophyll a, Chl $b$ = Chlorophyll b, Chl $a+b$ = Total chlorophyll, Cart = Carotenoids, $F_o$, $F_v$, $F_m$, $F_o/F_m$ and $Fe/Fo$ = Chlorophyll fluorescence indices.

In addition, we have determined the pairwise correlations between all of the measurements (Figure 4). Pearson’s correlation tests showed that almost all the plantlet morphological/biomass growth, chlorophyll pigments and nutrient contents had strong positive
correlations with each other, except for some other traits such as RWR, R_{dw}/S_{dw} and F_o, and the Chl a/b ratio. In turn, the rate of mycorrhizal colonization (Myc %) correlates emphatically with all the morphological/biomass features, chlorophyll pigments and mineral macro- and micronutrients (such as P, K, Mg, Fe and Zn) (at \( p < 0.00001 \)), Zn and RDW (at \( p < 0.001 \)), Cart and Fo/Fo (at \( p < 0.001 \)) and Fe, Fo/Fm, Na and Ca (at \( p < 0.05 \)). Out of the 496 correlation tests, 81 were negative, with just twenty-eight being significant. Twenty-four were recorded for chlorophyll a/b with all the variables except F_o, Fr/Fo, Fo/Fm, SFW/SDW, RWR and the R_{dw}/S_{dw} ratio. Three were identified for Fo with Fm, Fr/Fo and Fr/Fm (\( p < 0.01 \)), and one was marked between the root-to-shoot ratio and SRW (\( p < 0.0001 \)). One was observed between R_{dw}/S_{dw} and SDW (\( p < 0.05 \)) (Figure 4).

![Figure 4. Pearson correlation matrix representing by heatmap illustration of all measured parameters. Each box's color intensity is directly commensurate with the Pearson's r correlation coefficient-value between every two variables in row and column. R value ranges between −1 and 1 as presented in the heatmap legend. ns, *, **, ***, **** indicate no significant correlation, significant correlation at \( p < 0.05 \), \( p < 0.01 \), \( p < 0.001 \) and \( p < 0.0001 \) confidence level, respectively. Abbreviations for all parameters are noted above in Figure 3.](image-url)

**4. Discussion**

This paper focuses on highlighting the potentially advantageous effect of AMF inoculation on caper plants’ adaptive response to different levels of soil water deficit. First of all, our findings show that the native AMF complex, originating from rhizospheric wild-caper soils in Morocco’s Safi region, successfully colonized all the inoculated C. spinosa plantlets. It remarkably boosted the chances and root colonization rate under stressful water-deficit conditions. Research by Liu and Ma [20] revealed that 39.15% is the topmost mycorrhizal infection rate (MC) of C. spinosa achieved by Glomus mosseae (G. mosseae) relative to that of Glomus versiforme (G. versiforme). At the same time, the native AMF complex, in the
present study, enhanced this proportion to reach 55.3 and 51.7% at 50% FC and 25% FC, respectively. It is conceivable to speculate that the richness and abundance of indigenous AMF spores existing in the caper plants’ rhizospheric soil may be thought to increase the extent and occasions for root colonization, thereby raising their MC. Comparably, Shi et al. [31] observed that MC rose in desert ephemeral plants as soil moisture levels lowered. They partly explain these MC rates by inferring that the AM fungi pathway function of obtaining soil water to relieve plant water stress was no longer obliged when the soil moisture level increased. Hence, the results of mycorrhizal dependency supported this conclusion (Figure 1). Bethlenfalvay et al. [41] revealed that WDS did not dwindle the rate MC of soybean roots by *G. mosseae*; however, in severely droughted plants, the biomass and length of the extra-radical mycelium (ERM) formed by AMF were significantly higher. Drought may impact mycorrhizal colonization in experimental designs, including potted plants, such as the one used in our work, by encouraging rather than reducing root colonization [42]. Jadrané et al. [27] also found similar results recently, as they revealed an elevated colonization rate in mycorrhized carob seedlings as water-deficit levels progressed. Indeed, our results are in line with those reported in Zhang et al.’s [25] research, where mixed AMF inoculation provides a more important benefit than inoculation by single AMF species for the growth of *Zenia insignia* plants, notably in the presence of drought stress. Numerous studies have proven a substantial improvement in plants’ and trees’ development and survival thanks to inoculations with the native AMF mixture, especially in stressed/degraded sites [26,34,42–44]. The use of native soil AM fungi may be a handy alternative source to commercial AMF inocula in sustainable or organic farming systems. It may also generate relevant economic and ecological benefits in these Mediterranean soil systems [45].

Overall, the AMF complex colonization makes it possible to hugely improve the development of both caper seedlings’ morphological and biomass traits, regardless of the soil FC level. Mycorrhized caper plantlets became stronger under both mild and extreme WDS. They produced more dry and fresh biomass, suggesting that mycorrhizal symbiosis positively impacts the host plant’s growth, which is consistent with those of previous findings [13,24,25,27,31,32,42–50]. Concomitantly, whether in the absence or presence of MFI, caper plants’ morphological development and biomass produced under well-watered conditions were largely unaffected by the reduced soil FC. This is partly explained by their morpho-anatomical and physio-biochemical adaptation mechanisms that enable caper plants to endure certain water pressure forms [8,10,14]. In fact, plant resistance to water stress can be categorized into species that escape, avoid or tolerate drought stress following the characteristics of their adaptive mechanisms [51]. *C. spinosa*, as a species with the traits of xerophytic plants, is designated a drought-tolerant species. Among its tolerance mechanisms, Gan et al. [13] showed that wild caper uses various methods to respond to droughts, such as adjusting their root, stem and leaf structures.

Another pivotal mechanism is that the wild caper can restrict water loss and extract water from its surroundings thanks to its extensive/vigorous root system, quite dense cortical cell layers in both taproots and fibrous roots and a very high root-to-stem ratio (*R*<sub>dw</sub>/*S*<sub>dw</sub>) [8,9,14]. Additionally, when caper plants were grown at 50% FC rather than 100% FC, WDS boosted the root length (RL) by 70% [18] or remained unaffected in another piece of research [52]. In watermelon, for example, both the *R*<sub>dw</sub>/*S*<sub>dw</sub> and RL increased during WDS, with the rise being huge in +AMF seedlings [33]. As with our findings, WDS does not influence either the SFW or the SDW but considerably increases the RFW and the RDW as WDS grows [52]. After 4–5 months of development, the root system of the wild caper may account for up to 62.5% and sometimes 65% of the total plant biomass [3,10,53]. This proportion of root biomass is consistent with our results and is up to 71–75% under drought conditions. Remakably, based on the obtained *R*<sub>dw</sub>/*S*<sub>dw</sub> ratio and RWR values at each level of WDS, we specifically observed that biomass is allocated to roots and shoots in roughly the same way in caper plantlets grown, whether in the absence or existence of AMF complex.
Although this biomass-partitioning rate did not differ in both treatments, AMF complex colonization greatly enhances both the above and belowground parts’ weights. In fact, drought resistance is bolstered by a rise in the R<sub>dw</sub>/S<sub>dw</sub> ratio caused by modifications in sugar partitioning, metabolism and transportation [54]. The Rdw/Sdw adjustment allows for a more efficient use of soil resources and improves the plant’s ability to withstand water stress [23]. In this environmental context, with the insufficiency of mineral elements, plants often devote the utmost of their biomass to the root compartment as an acclimation reaction [55]. Thus, this is explained by the theory of optimal partitioning, which states that plants must assign biomass to the vegetal organ that obtains the limited resources [56]. As a matter of fact, in uninoculated caper plantlets, the proportion of the root biomass relative to the total plant biomass grew somewhat. Then, it permitted both the R<sub>dw</sub>/S<sub>dw</sub> and the RWR to augment insignificantly slightly compared with the AMF-inoculated ones. This was conducted morphologically via the uninoculated plants’ economic tactic by reducing or preventing the development of branches and hence the number of nodes, principally under water constraints of 50 and 25% FC. On the contrary, at these FC ones, inoculation with the AMF complex made it possible to retain the same number of branches and nodes developed under well-watered conditions and, more than that, enabled a boost in the total plant traits and biomass present both above and below ground. AM inoculation would result in decreases in the R<sub>dw</sub>/S<sub>dw</sub> ratio through ameliorating the nutrition status of the plant species, and that this would occur irrespective of the fitness outcome of the symbiosis for the plant. Therefore, low R<sub>dw</sub>/S<sub>dw</sub> ratio values in AMF-mycorrhized caper plants may suggest the plant’s ability to withstand the effects of water stress perfectly, negating the requirement for greater root biomass [57].

In this study, AMF complex inoculation had a more useful impact on biomass growth under mild and severe drought levels than under well-watered conditions in C. spinosa seedlings. Even though AMF benefits plants heedlessly of soil moisture levels, Basyal and Emery [25] show that it is most beneficial at low-soil moisture levels by growing aboveground biomass and modifying many root architectural aspects, implying that the mycorrhizal association gains less at high soil moisture conditions. In conditions such as drought, AMF may change the root architecture, such as empowering the lateral root (LR) development or extending the LR and diameter, which may give more surface area and make it easier to absorb water and nutrients [25]. For example, drought stress importantly increased the root-hair length, density and diameter in taproot and lateral roots in mycorrhizal and non-mycorrhizal trifoliate orange (Poncirus trifoliata) plantings; further, inoculation by Funneliformis mosseae or Diversispora versiformis meaningfully raises all the root-hair features in undroughted and far more in droughted seedlings by upregulating/increasing the root endogenous phytohormones levels [49]. Drought tolerance in mycorrhized plants may be ascribed primarily to the vast layer of soil exploited by roots and the AM fungi’s ERM [29]. Indeed, the mycorrhizal relationship improves the host plants’ exploration of water and nutrients mainly through expanding the mycelial network in the rhizosphere zone, ultimately facilitating increased growth and biomass accumulation [46].

Besides being a conspicuous factor contributing to plant biomass growth in this experiment, the AMF complex colonization has also considerably boosted the caper plants’ nutrient uptake and hence their mineral composition. Caper seedlings grown in AMF colonized soil exhibited considerably higher levels of macronutrients such as phosphorus (P), potassium (K<sup>+</sup>) and magnesium (Mg<sup>2+</sup>) as well as micronutrients such as zinc (Zn) and iron (Fe) contents in their aboveground tissues at all soil moisture stress levels studied than those grown in non-colonized soil. Previously, in the presence of G. mosseae and G. versiforme, both the aerial and root parts of the AMF-inoculated C. spinosa plants showed a considerable rise in P and nitrogen (N) content [21]. Interestingly, according to Pugnaire and Esteban [21], supplementation with chemical fertilizers of inorganic phosphate (Pi) significantly enhanced the dry biomass production of caper shrub leaves (~61%) and P (~33%), Ca (~20%) and Mg (~30%) concentrations in nutritional tissue, implying that it
is a growth-limiting nutrient in addition to the N element. Therewith, the same authors also reasoned that the caper shrub plants’ deep mycorrhizal root system enables them to thrive effectively in extremely infertile soils, maximize mineral uptake, aid in water absorption and withstand environmental stress. In this respect, our results have exclusively substantiated this viewpoint. Compared to their AMF counterparts, the nutritional status of mycorrhizal caper plantlets makes us acknowledge that the indigenous AMF complex could behave as a biostimulant/biofertilizer with a high-profitable function in nutrient-deficient soils. Indeed, the P content increased as the soil moisture decreased in both the mycorrhized and non-mycorrhized caper plants, but substantially only in the AMF-inoculated plantlets under severe drought. In some contexts, when there is not sufficient water in the soil, it has been found that the plant roots can obtain the phosphorus they need. This is perhaps made prominent by the contribution of AM fungi [24,29,58]. In fact, AMF-colonized plants ideally have two paths of obtaining P and other mineral elements from the soil, the direct route conducted by root hairs/epidermis, and indirectly via a mycorrhizal pathway by means of either internal or external AM fungi hyphae into root cortical cells, where hyphal and/or arbuscules coils offer symbiotic interfaces [59,60]. It is estimated that the ERM network of AM fungus in the soil increases the absorption surface area by up to 100 times more than the root hair. This mycelial network extends far beyond the zone of depleted Pi. It may enter and exploit soil pores that are physically unreachable to roots, thus constituting an effective nutrient-absorption net [58]. AM fungus may provide up to about 70–90% of the plant’s P requirements [22,59]. In AMF-inoculated caper seedlings, as the soil moisture decreases, the AMF-colonization rate rises (Figure 1), the root system continues to grow greatly (Table 1) and, in fact, the ERM network is often elongating further; thus, that is why the two P absorption pathways evoked above will permit accumulating a high level of this major element. Alike, Püschel et al. [61] suggested that the direct hyphal absorption of P, as well as AMF’s indirect modification of substrate hydraulic properties, were responsible for a greater instantaneous P uptake by +AMF plants growing under mild/low moisture substrate levels in his experiment. It is expected that numerous essential P roles in cell and whole plant development processes (e.g., formation of roots, cell division, enlargement, respiration, photosynthesis, energy storage and transfer) improve with increased P in moderately/extremely water-stressed mycorrhizal caper plants. In this regard, our findings reveal that the P concentration and mycorrhizal colonization rate have a statistically very significant positive correlation with each other, as well as with all the morphological and biomass traits, chlorophyll pigments and mineral nutrients (Fe, Zn, Mg and K). Similar to P, the inoculation of caper plantlets with MFI substantially raised K⁺ content at all the soil moisture levels, whereas all the levels of the WDS factor do not influence the K⁺ concentrations in the two plant treatments (with or without MFI). Sometimes, the K⁺ content may even rise if the drought is low and short in both intensity and duration [62], denoting that these two criteria in our experiment do not stringently constitute the most severe drought contexts that may affect the absorption, transport and accumulation of K⁺ in caper seedlings. It has been observed that the higher the K⁺ absorption is, the better the drought-stressed plants may efficiently exploit soil moisture, as seems to be the scenario for the caper seedlings in our experiment when AMF inoculum is applied at all the WDS conditions. Hence, numerous critical functions in AMF-colonized caper plants, particularly those growing under low soil moisture, are expected to improve as K⁺ levels rise. Potassium’s beneficial and protective effects on WDS tolerance include the promotion of root growth, which leads to an increased nutrient and water absorption by plants, the reduction in transpiration water loss, the maintenance of osmotic potential and cell turgor, the regulation of stomatal performance and the enhancement of the photosynthesis rate, as well as the maintenance of a high pH in the stroma and against the photooxidative damage to chloroplasts [63]. The considerable accumulation of K⁺ in caper species has already been reported in the literature before. Among the twenty-one macro and micro minerals measured in samples of seeds, flower buds, caperberries and young shoots of a caper shrub, Özcana [64] found that the K⁺ concentration was greatest in the majority of these plant
organs. Although K\(^+\) content is important in our study, it comes into order after the Na\(^+\) element. As a result of this observation, we can think of the possibility of a role substitution strategy between these two minerals, at least in the context of our experimental design and the soil nature. Na\(^+\) may fulfill some of the potassium’s physiological functions, such as an osmoticum in the vacuole. Additionally, Na\(^+\) uptake systems may be relevant for plant development when K\(^+\) availability is limited [65]. According to Pugnaire and Esteban [21], after chemical P fertilizer treatment, K\(^+\) and P have a significant antagonistic link; hence, the considerable rise in P in mycorrhizal caper plants may have changed the potassium balance. Indeed, the rhizosphere soil sampled, which we used as one-half of the substrate in this experiment, is typical of the caper plant’s soil in Morocco’s most significant area for its existence and production. Of particular interest to note, C. spinosa, which originated precisely in Morocco’s Safi region where the seeds and soil samples for this study were collected, is already internationally recognized for its high biological activity potential and rich bioactive chemicals when compared to those found in other Mediterranean areas [2,66]. Admittedly, this hints that the region’s soil physicochemical and biological characteristics (Safi, Morocco) remain distinct and unique, making C. spinosa grow and be characterized by required and valuable properties. Due to these and other considerations, in order to explore the favorable impact of native AMF and caper plantlets’ association under WDS, we opted to employ the rhizospheric soil as the principal source of AMF inoculum and as a cultivating substrate. The noticeable buildup of Na\(^+\) recorded in the current study is presumably attributable, first and foremost, to the permanent salinization of soils resulting from anthropogenic and/or natural factors in most agricultural and marginal land-soils, especially in semi-arid/arid Mediterranean environments [67,68], similar to the one in the Morocco-Safi area. Accordingly, C. spinosa may thrive in drought-prone soils and contain a certain degree of salt, as previously documented [17,18,52]. On the other hand, several evaluative studies found that chloride sodium (NaCl) plays a pivotal role in some species drought tolerance due to the plants’ capacity to absorb/accumulate high amounts of Na\(^+\) in the leaves and compartmentalize them into vacuoles, as well as the usage of Na\(^+\) as a low-cost physiological osmoregulator to diminish the osmotic potential [69–73]. Otherwise, neither WDS levels nor AMF-complex inoculation had a discernible effect on the Na\(^+\) and Ca\(^{2+}\) uptake/concentrations in dry caper shoots. Regardless, +AMF plants acquire these two nutrients at a higher rate than −AMF ones under all soil moisture levels. AMF colonization, for example, enhanced Ca\(^{2+}\) content in water-stressed citrus seedlings [74]. However, other research, such as that conducted by Kabir et al. [75], found that it had no impact. In our study, the Ca\(^{2+}\) content is also paramount compared to the other mineral elements. The Na\(^+\) content comes first, with Ca\(^{2+}\) larger than K\(^+\) in uninoculated plants and vice versa in those inoculated. This quantity variation between these two minerals grows with WDS in both +AMF seedlings and their control counterparts. The remarkable Ca\(^{2+}\) quantity observed in leaves’ dry matter is conceivably explained by the calcareous nature of the soil from which we took the rhizospheric soil samples, as well as by the calcilolous strategy that characterizes caper species. Pugnaire and Esteban [21] found the same and pointed out that high Ca\(^{2+}\) in addition to K\(^+\) levels will help to maintain hydric balance (water conservation and economy) and thorny stems in caper shrub. Moreover, several works, such as that by Khushboo et al. [76], reveal that exogenous Ca\(^{2+}\) application in plant species reduces the harmful effects of drought stress by regulating antioxidant machinery and improving osmoprotectant accumulation. It is implicated in signaling anti-drought responses. Preventing physiological disorders induced by adverse environmental circumstances is more manageable when optimizing each organ’s Ca\(^{2+}\) content and distribution in +AMF and −AMF plants [77]. Unlike Na\(^+\) and Ca\(^{2+}\), the AMF complex meaningfully augmented Fe\(^{2+}\) and Zn\(^{2+}\) amounts at all the WDS levels. Since Zn\(^{2+}\) deficiency is widespread in semi-arid–arid zones owing to the soil’s alkalinity/calcareousness, high pH and low organic matter, all of which reduce the Zn\(^{2+}\) phytoavailability and solubility [78], and because these same soil categories are also Fe\(^{2+}\) deficient, accounting for roughly one-third of the world’s cultivated soils [79], this
improvement of Zn\(^{2+}\) and Fe\(^{2+}\) concentrations by inoculating caper plantlets with AMF is, therefore, enormously coveted. This is especially important when considering that these are the same soil properties where *C. spinosa* culture intensification occurs worldwide. According to previous research, Zn\(^{2+}\) and Fe\(^{2+}\) may be mobilized and taken up by AM fungi hyphae, thereby translocated to the host plants to raise these elements’ amount in the presence, or not, of WDS [22,30,48,80]. More outstandingly, it has been demonstrated that AMF-microbial (four *Glomus* spp.) supplementation markedly improved the Fe\(^{2+}\) and Zn\(^{2+}\) contents in sunflower roots and shoots under Fe deficiency conditions while also mitigating the severity of Fe-deficient symptoms by increasing ferric reductase activity and the corresponding gene’s expression as well as optimizing CAT and SOD activities [75].

Interestingly, the +AMF caper plantlets had considerably higher magnesium (Mg\(^{2+}\)) concentrations than the non-mycorrhizal ones at all the soil moisture levels, notably when WDS was severe, as did P, K\(^{+}\) and Fe\(^{2+}\). Wu and Xia [74] obtained similar findings, in which MFI improved the Mg\(^{2+}\) content of seedlings subjected to WDS more than well-watered citrus seedlings. Figure 4 shows that all the mineral nutrient concentrations, notably Mg\(^{2+}\) and Fe\(^{2+}\), are strongly and significantly correlated with all the chlorophyll pigments, as well as chlorophyll fluorescence indicators (*Fo/Fm* and *Fo/Fo*). Fe\(^{2+}\) is, in fact, an indispensable component of electron carriers in the photosynthetic apparatus, and a shortage in this element has been shown to reduce the chlorophyll score, *Fo/Fm* and photosynthesis performance index in the leaves. In contrast, AMF supplementation restored these photosynthesis parameters to their pre-deficiency levels [75,81]. Since Mg\(^{2+}\) is a major chlorophyll component and is required for Rubisco activation (among other things), plants deficient in Mg manifest a decrease in *Fo/Fm* and a prolonged induction of photosynthetic parameters [81]. Mg\(^{2+}\)-deficient citrus plants increased in *Fo* and *Fm* levels while lowering in *Fo*, leading to lower *Fo/Fo* and *Fo/Fm* ratios, which often trigger thylakoid structural alterations as well as photooxidative/photoinhibitive damage [82]. In our study, *Fo* peaked in non-mycorrhizal seedlings, while *Fm*, *Fo/Fm* and *Fo/Fo* hit their peak in AMF-colonized plants, demonstrating the AMF complex’s beneficial role in boosting photosynthetic performance. The significant improvement in *Fo/Fm* was made evident by the *Fo/Fo*, revealing that it is a better measure for discerning minor differences in PSII’s photosynthetic performance [57]. This gain became obvious and significant for the *Fo/Fm* and *Fo/Fo* barely under moderate and severe WDS conditions. Studies have shown that inoculation with AMF boosts photosynthetic activity and PSII performance under drought contexts by maintaining a better chloroplast ultrastructure, increasing the Rubisco concentration and diminishing the free radical buildup [24,34]. While at 25 and 50% FC, the observed reduction in *Fo/Fm* and *Fo/Fo* in the absence of AMF implies that WDS altered PSII’s photochemical efficiency and electron transport chain, possibly contributing to photoinhibition damage. At 75% FC, there is no substantial difference in all the chlorophyll fluorescence parameters between +AMF and −AMF plantlets. We also noticed that increasing the WDS gradient did not significantly affect *Fo/Fm* or *Fo/Fo*, either in the mycorrhizal or non-mycorrhizal seedlings. On this matter, even when WDS was induced by PEG treatment, *Fo/Fm* values decreased slightly with no notable difference between the control and droughted *C. ovata* leaves [83,84]. Additionally, there were no symptoms of photooxidative stress in caper leaves throughout the growing season (summer) due to a high *Fo/Fm* and xanthophyll cycle function [10]. Moreover, Zuo et al. [13] previously reported that the caper’s photosynthesis rate (Pn), stomatal conductance (Gs), transpiration rate (E) and WUE were all better and, at the same time, superior to those of other desert plant species found in the same type of habitat. Furthermore, it is worth noting that AMF plant colonization favorably stimulates all of these GEPs, most notably under conditions of water limitation, as shown by Augé et al.’s meta-analysis [85]. Accordingly, the magnitude of this impact will be investigated in the future by examining the GEP in an AMF-inoculated caper shrub. In contrast, the biosynthesis and breakdown of chlorophyll are critical to the photosynthesis of plants because chlorophyll plays a vital role in absorbing and converting light energy [17]. Chlorophyll status is a key indicator for determining...
a plant’s photosynthetic efficiency and susceptibility to environmental stress. Our study detected a rise in all the chlorophyll pigments concentrations in *C. spinosa* seedlings with and without mycorrhizal symbiosis in response to increasing WDS levels, which is consistent with prior studies [52]. A previous study found that different parts of *C. spinosa* are rich in carotenoids in addition to tocopherols compounds, which might be a strategy of this species to deal with oxidative stress under stressful circumstances throughout the summer [6]. Remarkably, the AMF inoculation of caper plants significantly increases the total chlorophyll at all the WDS treatments, although the total carotenoid under severe WDS (25% FC) is greatly improved. Comparably, mycorrhizal symbiosis was observed to boost the accumulation of photosynthetic pigments, especially carotenoids and anthocyanin, in the leaves of two lettuce cultivars, with better improvement under water stress than ideal irrigation, according to a prior study [42]. By acting as non-enzymatic scavengers against the excessive accumulation of reactive oxygen species, increasing the carotenoid content helps plants battle the photodegradation and photoinhibition of pigments under stressful circumstances [31].

5. Conclusions

The native arbuscular mycorrhizal fungi (AMF) complex’s advantageous influences on the caper plant’s growth characteristics were examined in this study, giving insight into how they acquire nutrients and adapt physiologically to cope with extreme water deficit circumstances. Overall, the inoculation of caper seedlings with a native AMF mixture during moderate (50% FC) and severe (25% FC) WDS has a significant beneficial effect on morphological growth, biomass production, nutrients uptake, chlorophyll pigments content and photosynthetic performance, thus greatly mitigating the detrimental influences of soil WDS. *C. spinosa* seems to be reliant on symbiotic relationships with its microbiota-mycorrhizal partners to survive perfectly in harsh Mediterranean environments, hence becoming more important when soil water levels drop, and soil quality deteriorates. The findings from this study may serve as a basis to develop a novel agronomic management approach for eco-friendly farming based on mycorrhiza technology to improve capers’ performance/production, yield and intensification in extremely droughted/degraded habitats and nutritionally poor soil, as well as reduce transplant shock in young seedlings. Nevertheless, thorough investigations might look at the effectiveness of specific AMF species or other inocula sources (e.g., a microbial consortium) in the presence of another abiotic stressor, as well as in conjunction with different caper cultivars’ experimental field conditions under a high intensity/period of stress.

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