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Response to Inoculation with Arbuscular Mycorrhizal Fungi of Two Tomato (*Solanum lycopersicum* L.) Varieties Subjected to Salt Stress under Semi-Controlled Conditions

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Abstract

Salinity is a major problem that seriously impacts agricultural production, particularly that of tomato (*Solanum lycopersicum* L.). However, the plant has the ability to associate with Arbuscular Mycorrhizal Fungi to better tolerate salt stress. Thus, thanks to the extension of the AMF hyphae, the hydro-mineral nutrition and the tolerance to excess toxic ions (Na^+ and Cl^-) of the plant are optimized. In this context, the contribution of AMF to the salt stress tolerance of two tomato varieties under semi-controlled conditions was studied. To do this, the frequency and intensity of mycorrhization, the relative mycorrhizal dependency, the survival rates, the aerial and root dry weights, the mineral (P, K^+, Na^+) and proline contents of the plants subjected to four levels of salinity [0, 70, 140 and 210 mM of NaCl] were evaluated. All the parameters assessed appeared to be dependent on the variety, the fungal strain and the NaCl concentration. With the *Lady Nema* variety, inoculation with the *Claroideoglomus etunicatum* strain at [NaCl 140 mM] resulted in the highest frequencies (54%), intensities (40.47%), and relative mycorrhizal dependencies (19.65%). This same symbiotic couple recorded high survival rates (55%) and aerial (2.03 g) and root (0.50 g) dry weights. Significant contents of K^+ (Leaves: 7.5 $mg{\cdot}g^{-1}$; Roots: 4.4 $mg{\cdot}g^{-1}$ of dry matter), P (Leaves: 15.15 $mg{\cdot}g^{-1}$ of dry matter) and proline (975 $nmoles{\cdot}g^{-1}$ of fresh matter) were

also recorded by this pair, with the lowest Na^+ contents (Leaves: 1.93 $mg \cdot g^{-1}$; Roots: 0.96 $mg \cdot g^{-1}$ of dry matter). For the *Mongal* variety, at [NaCl 140 mM], the highest frequencies (50.36%), intensities (35.14%) and relative mycorrhizal dependencies (43.95%) were obtained thanks to inoculation with *Rhizophagus fasciculatus*. The highest survival rates (59%) and aerial (2.58 g) and root (0.79 g) dry weights were also obtained with this symbiotic couple. The contents of K^+ (Leaves: 6.1 $mg \cdot g^{-1}$; Roots: 3.09 $mg \cdot g^{-1}$ of dry matter), P (Leaves: 12.49 $mg \cdot g^{-1}$ of dry matter) and proline (942 $nmoles \cdot g^{-1}$ of fresh matter) the most important and those in Na^+ the lowest (Leaves: 2.03 $mg \cdot g^{-1}$; Roots: 1.53 $mg \cdot g^{-1}$ of dry matter) were also recorded for this same pair. Thus, the best fungal partner for the *Lady Nema* variety is *C. etunicatum*, followed by *F. mosseae* and *R. fasciculatus*, while for the *Mongal* variety it is *R. fasciculatus*, followed by *C. etunicatum* and *F. mosseae*.

Keywords

Solanum lycopersicum, Salt Stress, Arbuscular Mycorrhizal Fungi, Growth, Phosphorus, Potassium, Sodium, Proline, Tolerance

1. Introduction

One of the factors strongly limiting the development of plants in semi-arid zones is the process of land salinization. The impact of salinity is reflected in many plants that are not adapted or not very tolerant of a drop in their vegetative potential [1]. Salinity reduces plant growth, imposes ionic and osmotic effects and induces oxidative stress, which results in the disruption of hydromineral nutrition due to excess salts in the root zone [2]. Toxic effects also include disruption of the structure of enzymes and other macromolecules, damage to cell organelles and plasma membrane, disruption of photosynthesis, respiration and protein synthesis [3]. In general, agricultural production in saline areas largely depends on the success of the germination and emergence phases of seedlings as well as the efficiency of the reproduction phase. Most crop plants are glycophytes and their responses to salinity appear to be species and variety specific within a species [4]. However, previous studies have shown that inoculation of plants with selected beneficial soil microorganisms such as AMF could improve their tolerance to salinity [5]. Indeed, several plant species, such as tomato (*Solanum lycopersicum* L.), have the ability to associate with arbuscular mycorrhizal fungi [6]. AMF are able to establish a symbiosis with nearly 80% of plants, most of which are agricultural and horticultural plants. Thanks to the development of a network of filaments, the symbiotic associations allow the plant to increase its contact surface with the soil, thus allowing a larger surface for prospecting the soil [7]. The mineral elements are transmitted from the fungus to the plant in exchange for a transfer of carbon from the host plant to the fungus. This mutually beneficial symbiotic association of fungi with plant roots contributes to improv-

ing the use of water and nutrients, especially those with low mobility in the soil, and increases the tolerance of plants to various abiotic stresses [5]. AMF, therefore, improve host physiological processes such as the water and mineral absorption capacity of plants by increasing the hydraulic conductivity of the roots and by favorably adjusting the osmotic balance and the composition of carbohydrates [8]. Several authors have shown that exploiting the microbiological potential of soils, in particular that of arbuscular mycorrhizal fungi, could promote the adaptation of plants to saline environments [7]. Thus, several studies have shown a significant improvement in growth, water nutrition, root and aerial biomass of tomato plants inoculated with AMF and grown in saline conditions [8]. Mycorrhization also improves the levels of phosphorus, nitrogen, potassium and proline (osmoregulator) in tomato plants under salt stress while decreasing those of sodium [9]. This is mainly regulated by the supply of nutrients to the root system and the increase in transport (uptake and/or translocation) by the AMF [10]. Work carried out in the greenhouse on tomato varieties has shown a significant improvement in growth and mineral nutrition, root and aerial biomass thanks to inoculation with AMF [11]. Mycorrhizal frequencies and intensities are also influenced by salt resulting in an increase in mycorrhizal dependency with increasing salt concentrations. The attenuation of salt stress by AMF would result from a combination of nutritional, biochemical and physiological effects [12].

Thus, a better knowledge of the specific relationships between plants and mycorrhizal fungi is necessary for adequate and optimal use of these microsymbionts to increase the tolerance of plants to salinity. This study was undertaken, under semi-controlled conditions, to evaluate the beneficial or non-beneficial effects of mycorrhization with selected strains on the growth of plants of two tomato varieties (*Solanum lycopersicum* L.) subjected to increasing concentrations of NaCl [0, 70, 120 and 240 mM] based upon the screening results previously obtained [13]. These two varieties of tomato (*Lady Nema* and *Mongal*) were selected for this study because they appeared more tolerant to salinity during *in vitro* tests carried out on a selection of five varieties among the most cultivated in Senegal [13]. This will allow identifying the best symbiotic couples to optimize tomato growth and productivity in Sahelian areas affected by saline stress.

2. Material and Methods

2.1. Plant Material

The plant material (**Table 1**) consists of seeds of the two best performing hybrid tomato varieties (*Solanum lycopersicum* L.) identified during work under *in vitro* conditions, namely the *Lady Nema* and *Mongal* varieties [13]. The seeds were supplied by the company Tropica Sem-Senegal (Technisem Novalliance Group, 2019), located in Dakar city. The characteristics of the seeds and the storage conditions are similar to those used during the *in vitro* study of salt stress [13].

Table 1. Origins and characteristics of the tomato varieties (Tropica Sem, 2019).

Varieties	Origin	Characteristics
Lady Nema	Tropica Sem	Adapted to the rainy and hot season, determined growth, good leaf cover, good yield, earliness of 75 - 80 days, good tolerance to nematodes, CMV (Cucumber Mosaic Virus), TYLCV (Tomato Yellow Leaf Curl Virus), resistant to TMV (Tobacco Mosaic Virus) and *Fusarium*.
Mongal	Tropica Sem	Adapted to therainy and hot season, determined growth, very good vigour, excellent fruit set, earliness (65 days), resistant to TMV (Tobacco Mosaic Virus), *Fusarium* and *Meloidogyne spp*.

2.2. Fungal Material

To evaluate the impact of fungal inoculation on the growth and development of tomato plants under salt stress, three strains of arbuscular mycorrhizal fungi were used. They come from the collection of the Joint Microbiology Laboratory (LCM, IRD/ISRA/UCAD**) of the ISRA-IRD research center in Dakar Bel-Air (Senegal). These *are Claroideoglomus etunicatum*, *Rhizophagus fasciculatus and Funneliformis mosseae* [14], whose old names were respectively *Glomus etunicatum*, *Glomus fasciculatum and Glomus mosseae*. The references of the strains are specified in **Table 2**.

To obtain enough inoculum, each pure AMF strain was propagated under a potted shadehouse using a mycotrophic plant, maize (*Zea mays* L.), in Sangalkam soil sterilized at 120˚C for 2 hrs. The composition and the physico-chemical characteristics of the Sangalkam soil are listed in **Table 3**. After 3 months of cultivation, the roots and the culture substrate were collected to evaluate the density of the spores on the one hand [15] and, on the other hand, the root colonization rate for each AMF strain [16] [17]. The maize roots colonized by each AMF strain were then cut into fragments of about 1 cm and mixed with the culture medium containing spores and hyphae, to constitute the fungal inoculum.

2.3. Culture Substrates

The soil taken from Sangalkam (**Table 3**), located 50 km from Dakar (approximate GPS position: Latitude, 14˚78'11"N, Longitude, −17˚22'78"W), served as a substrate for the greenhouse study of the effect of mycorrhizal fungi on the salt stress tolerance of tomato plants. The soil was taken three weeks before the experiments, from a horizon between 10 and 20 cm deep. It was sterilized in an oven at 120˚C for 96 hours to eliminate all native microflora.

2.4. Methods

2.4.1. Experimental Device and Culture Conditions

1) Experimental Device

The trial was conducted under shade at the Plant Biology Department (FST/UCAD**).

Table 2. References of the strains of arbuscular mycorrhizal fungi from the LCM** collection (IRD/ISRA/UCAD**).

Arbuscular Mycorrhizal Fungi	References	Abbreviations
Claroideoglomus etunicatum	[14] NCBI:txid937382 (Becker and Gerdemann BEG 176)	*C. etunicatum*
Rhizophagus fasciculatus	[14] NCBI:txid47032 (Thaxter *sensu* Gerdemann DAOM 227 130)	*R. fasciculatus*
Funneliformis mosseae	[14] NCBI:txid27381 (Nicolson and Gerd.; Gerd. and Trappe DAOM 227 131)	*F. mosseae*

**IRD: Institut de Recherché pour le Développement; ISRA: Institut Sénégalais de Recherches Agricoles; LCM: Laboratoire Commun de Microbiologie; UCAD: Université Cheikh Anta Diop.

Table 3. Physico-chemical characteristics of Sangalkam soil [18].

Component elements	Content for 100 g of soil
Sand	88.8%
Silt	5.8%
Clay	5.4%
Organic material	0.6%
Total carbon	0.3%
pH	5.33
pH KCl	4.4
CE (µs·cm^{-1})	121.6
Nitrogen (%)	0.051
Pass (ppm)	62.244
Na^+ (meq/100g)	0.465
K^+ (meq/100g)	0.749
Fe^{2+} (ppm)	0.251
Mn^{2+} (ppm)	0.002
Cu^{2+} (ppm)	0.00001
Zn^{2+} (ppm)	0.01
C/N Ratio	14%
Calcium total	1.03 ppm
Magnesium total	0.30 ppm

Na^+: Sodium; K^+: potassium; Fe^{2+}: iron; Mn^{2+}: manganese; Cu^{2+}: copper; Zn^{2+}: zinc; Pass: Available phosphorus.

The effects of inoculation with AMF strains were studied in the *Lady Nema* and *Mongal* varieties which appeared to be the most tolerant to salt stress following the test under *in vitro* conditions [13].

The adopted experimental set-up is a randomized block with 3 factors: inoculum, variety, and salt stress (**Figure 1**).

- The inoculum factor has four levels: un-inoculated controls and plants inoculated with strains of *Claroideoglomus etunicatum*, *Rhizophagus fasciculatus* and *Funneliformis mosseae*.

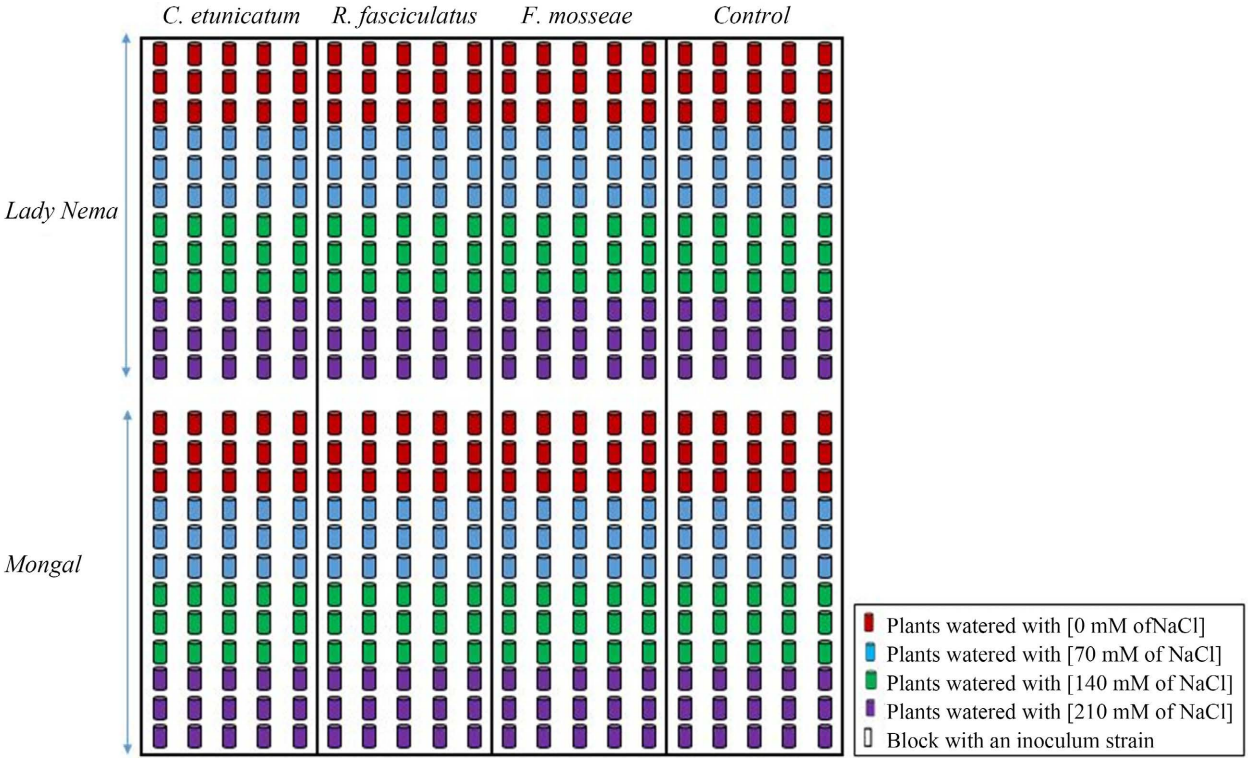

Figure 1. Experimental device for the test under shade in semi-controlled conditions.

- The variety factor has two levels: *Lady Nema* and *Mongal*.
- The salt stress factor has four levels of [NaCl]: 0, 70, 140 and 210 mM [13].

For each salt stress condition, a total of 15 plants/variety/inoculation condition was used, *i.e.*, 480 plants. Plants were watered to field capacity every two days and maintained under these conditions for 2 weeks before applying each concentration of NaCl.

2) Culture Conditions

The containers consisted of black polyethylene bags (30 cm × 13 cm) filled with 2 kg of substrate. The sowing of the seeds, initially soaked for 2 h, was done by sowing 2 seeds per bag. Thinning, consisting of leaving one plant per bag, was carried out after emergence, *i.e.*, two weeks after sowing. The duration of the experiment, carried out entirely under semi-controlled conditions under shelter, was 3 months.

The inoculation was carried out at the time of sowing by providing 20 g of inoculum of the appropriate strain. The inoculum was characterized by a mycorrhization frequency of at least 85% and a spore density of approximately 40 for each fungal isolate. It was brought all around the seeds to a depth of 1 - 3 cm.

The experiments related to mycorrhization took place under shade from December 2020 to February 2021. The trial was conducted to allow good growth of the tomato plants (minimum and nocturnal thermal amplitudes of 21˚C to 24˚C and maximum and diurnal thermal amplitudes of 24˚C to 27˚C, respectively). No rainfall was recorded during the experiments.

2.4.2. Parameters Measured

1) Mycorrhization Parameters

At the end of the experiment, the plants were harvested and their roots were carefully cleared of the soil. The roots were thoroughly rinsed with water to remove adhering sand particles. Root colonization was observed after staining according to the technique developed by [16].

The histological examination was carried out under an optical microscope at 100 magnification, by mounting between slide and coverslip, 20 fine fragments of roots approximately 1 cm long for each plant, selected at random. The fragments were crushed with a few drops of glycerol. The presence of AMF structures such as hyphae, vesicles and arbuscules in the roots makes it possible to estimate the level of colonization of the root samples.

The intensity and frequency of mycorrhization were then evaluated by the method of [17].

- The frequency of mycorrhization (F) was evaluated without considering the stage of extra- and intra-root development of the symbionts. Only the presence or absence of mycorrhizal propagules is counted. It was calculated by the following formula:

$$F(\%) = \left[\text{number of mycorrhizal fragments} / \text{Total number of fragments}\right] * 100 \quad (1)$$

- Depending on the importance of colonization, a class is assigned to the root fragment and the intensity of mycorrhization is assessed as follows:

$$M(\%) = \left[95n5 + 70n4 + 30n3 + 5n2 + n1\right] / N \quad (2)$$

$n5$, $n4$, $n3$, $n2$ and $n1$ designate respectively the numbers of fragments of class 5, 4, 3, 2 and 1 and N is the number of fragments observed.

- Mycorrhizal dependency (MD) is defined by [19] as the degree to which a plant is dependent on mycorrhizal status in order to grow and yield at maximum at a given level of soil fertility. Relative mycorrhizal dependence (RMD) expresses the degree to which a plant responds to mycorrhizal inoculation under fertile soil conditions. It was calculated using the method of [20] according to the following formula:

$$\text{RMD}(\%) = \left[\frac{\text{Total biomass of mycorrhizal plants} - \text{Total biomass of control plants}}{\text{Total biomass of mycorrhizal plants}}\right] * 100 \quad (3)$$

2) Agro-Morphological Parameters

After 3 months of cultivation, the plants were carefully harvested from each polyethylene bag. Their roots were thoroughly rinsed with tap water to remove adhering sand particles. The agro-morphological parameters determined were the fresh and dry weights of the aerial and root parts. After separation of the aerial and root parts, their biomasses were determined with a Sartorius precision balance (accuracy: 0.0001). The different parts were then dried in an oven (Binder brand) for 120 h at a temperature of 80˚C ± 0.5˚C, before weighing the dry biomass of the aerial and root parts, respectively.

For each saline treatment and variety, the plant survival rate (PSR) was calculated as follows:

$$\mathrm{PSR}(\%) = [\text{Number of plants having survived} / \text{Total number of plants tested}] * 100 \quad (4)$$

This criterion was used to rank and classify tomato varieties according to their ability to tolerate salt stress.

3) Determination and Evaluation of Mineral Contents

- The determination of sodium (Na^+) and potassium (K^+) was carried out according to the method used by [21]. The fresh samples were rinsed three times with distilled water and dried in an oven at 70˚C for 48 h. After grinding the samples, 0.2 g of dry matter was incinerated in an oven at 500˚C for 6h. The ashes were collected and diluated into HCl. Thanks to an atomic absorption spectrophotometer (BK-AA320N, precision: ±0.5 nm), the Na^+ and K^+ contents were determined, respectively at λ = 589 nm and λ = 766 nm.
- The phosphorus (P) content was determined using Sodium Molybdate [22]. A 0.25 mL aliquot of the samples was used for the determination of Na^+ and K^+. It was added to 1.25 mL of Sodium Molybdate reagent (2.5%) and Hydrazine Sulphate (0.15%), and 1 mL of distilled water, then boiled for 10 min. Subsequently, the samples were cooled before reading the optical density with a spectrophotometer at λ = 820 nm (Shimadzu UV-1700, precision: ±0.3 nm).
- To assess the effectiveness of AMF in mineral nutrition by improving the absorption of potassium to the detriment of sodium, the foliar and root K^+/Na^+ selectivity ratio (R) was calculated according to the following formula [23]:

$$R = K^+ \text{ content} / Na^+ \text{ content} \quad (5)$$

4) Biochemical Parameters: Determination and Evaluation of Proline Contents

To assess the NaCl tolerance levels of the two tomato varieties, the average proline contents accumulated by the plants were determined. The protocol described by [24] was used to extract and assay the proline. The extraction was carried out from a composite mixture of 100 mg of leaf segments from three plants per treatment. The concentration of proline was determined with a spectrophotometer (Evolution 300 UV-VIS, accuracy: ±0.15 nm) by measuring the optical density (OD) at λ = 520 nm. The proline contents were calculated and determined by the equation deduced from the calibration curve *i.e.*, standard calibration curve, constructed from a range of known and increasing proline concentrations from 0 to 800 µmoles.

2.4.3. Statistical Processing and Data Analysis

The collected data were subjected to a multiple comparison of the means and to an analysis of variance with three factors (inoculum × variety × [NaCl]) by the Student-Newman-Keuls test (SNK). The analyses were carried out according to a

general linear model by the R-4.0.5 software using the "*Agricoleae*" package. The differences between the means were compared using the Student-Newman and Keuls test, and the significance was determined at 95% confidence limits, *i.e.*, the significantly different means were discriminated by the SNK test at the p-value of 5%.

3. Results

3.1. Influence of Salt Stress on Plant Mycorrhization Parameters

3.1.1. Effect of Increasing [NaCl] on the Frequency of Mycorrhization

The results of the statistical analyzes relating to the impact of increasing NaCl concentrations and AMF strains on the frequency of mycorrhization of the plants revealed a strong significance of the interaction [NaCl] × AMF strain × Variety ($F = 162.17$; $P < 2 \times 10^{-16}$). Indeed, the frequency of mycorrhization of plants varies significantly with the increase in NaCl concentration (*Lady Nema*: $F = 1749$; $P < 2 \times 10^{-16}$; *Mongal*: $F = 3125$; $P < 2 \times 10^{-16}$; **Figure 2**). Un-inoculated plants revealed no root colonization by AMF hyphae.

For plants of the *Lady Nema* variety, the rates of decrease in the frequency of mycorrhization at [NaCl 210 mM] vary from 86% (*C. etunicatum*) to 91% (*R. fasciculatus*) while for those of the *Mongal* variety, they vary from 88% (*R. fasciculatus*) to 92% (*C. etunicatum* and *F. mosseae*). However, a slight increase in the frequency of mycorrhization of 1% (*C. etunicatum*) and 2% (*R. fasciculatus*) is noted with the plants of the *Mongal* variety at [NaCl 70 mM]. The frequencies of mycorrhization of plants of the *Lady Nema* variety are slightly higher than those of the plants of the *Mongal* variety, with respectively the most efficient strain of AMF. Indeed, plants of the *Lady Nema* variety inoculated with *C. etunicatum* recorded mycorrhization frequencies of 94.03%, 94.01%, 54.01% and 13.05%, respectively at [0, 70, 140 and 210 mM of NaCl]. Under the same salinity conditions, plants of the *Mongal* variety inoculated with the *R. fasciculatus* strain recorded mycorrhization frequencies of 90.24%, 91.69%, 50.36% and 10.86%.

3.1.2. Effect of Increasing [NaCl] on the Intensity of Mycorrhization

A strong significance of the interaction [NaCl] × AMF strain × Variety ($F = 64.694$; $P < 2 \times 10^{-16}$) emerged during the statistical analyzes concerning the impact of increasing NaCl concentrations and AMF strains on the intensity of mycorrhization of the plants. Indeed, the intensity of mycorrhization of the plants varies significantly with the increase in NaCl concentration (*Lady Nema*: $F = 944.1$; $P < 2 \times 10^{-16}$; *Mongal:* $F = 1025$; $P < 2 \times 10^{-16}$; **Figure 3**).

The mycorrhization intensity of plants decreases significantly with increasing NaCl concentrations. However, an exception is noted with the couple *Lady Nema*/ *C. etunicatum* which recorded an increase of 2% in the presence of [NaCl 70 mM]. In the *Lady Nema* variety, the plants inoculated with *C. etunicatum* recorded the highest mycorrhization intensities with 39.59%, 40.47%, 21.33% and

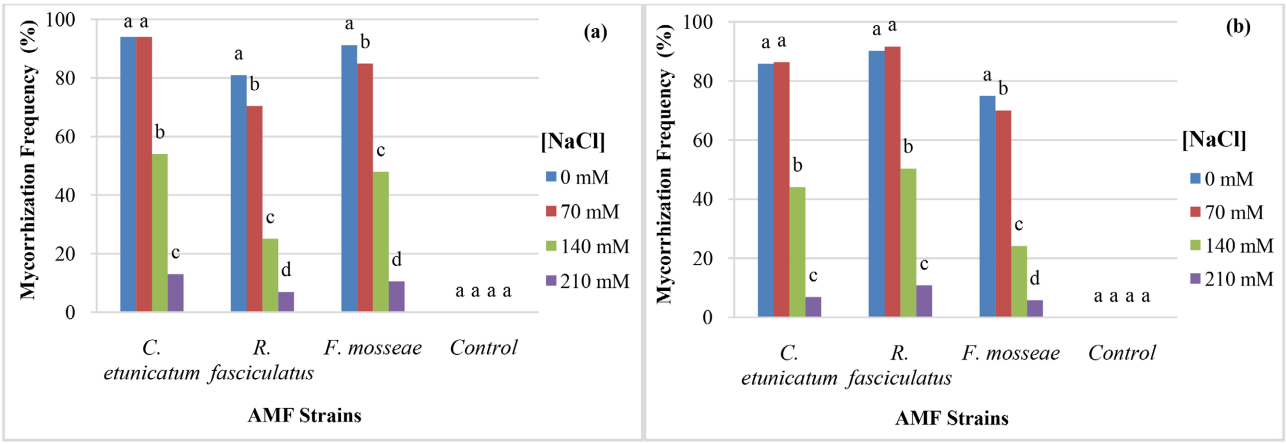

Figure 2. Effect of AMF strains on the mycorrhization frequency of plants of *Lady Nema* (a) and *Mongal* (b) varieties grown under increasing [NaCl]. For each inoculation condition, the letters a, b, c and d designate homogeneous groups for the comparison of the means according to the Newman-Keuls test at the 5% threshold.

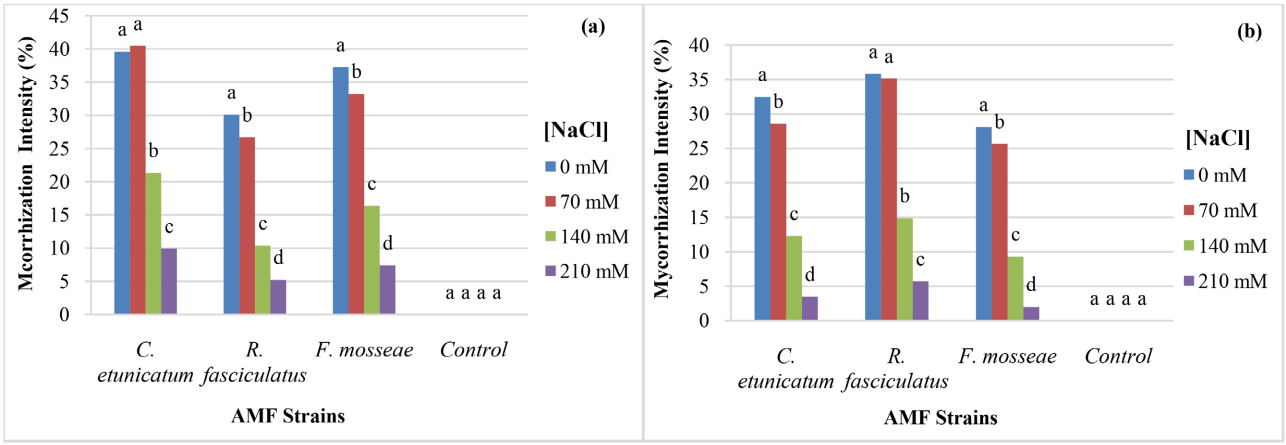

Figure 3. Effect of AMF strains on the mycorrhization intensity of plants of *Lady Nema* (a) and *Mongal* (b) varieties grown under increasing [NaCl]. For each inoculation condition, the letters a, b, c and d designate homogeneous groups for the comparison of the means according to the Newman-Keuls test at the 5% threshold.

9.92%, respectively at [0, 70, 140 and 210 mM of NaCl]. Under the same salinity conditions, the plants inoculated with the *R. fasciculatus* strain recorded the lowest intensities of mycorrhization (30.1%, 26.69%, 10.39% and 5.23%).

Regarding the *Mongal* variety, the plants inoculated with *F. mosseae* recorded the highest mycorrhization intensities, with 35.82%, 35.14%, 14.86% and 5.71%, respectively at [0, 70, 140 and 210 mM NaCl]. Plants inoculated with *F. mosseae* recorded the lowest intensities of mycorrhization under these same salinity conditions, with 28.11%, 25.65%, 9.3% and 2%.

3.1.3. Effect of Increasing [NaCl] on Relative Mycorrhizal Dependency

The variance analysis of the mycorrhizal dependency of the plants revealed a highly significant effect of the interaction [NaCl] × AMF strain × Variety ($F = 22.7$; $P < 2 \times 10^{-16}$). Indeed, relative mycorrhizal dependency varies significantly with increasing salt stress (*Lady Nema*: $F = 322.42$ and $P < 2 \times 10^{-16}$; *Mongal:* F =

314.76 and $P < 2 \times 10^{-16}$; Figure 4).

The mycorrhizal dependencies recorded with the AMF strains revealed positive and negative values relating to biomass gains or losses in the mycorrhizal tomato plants. Without saline constraint, the relative mycorrhizal dependencies of the plants to all the AMF strains are negative. The maximum dependency is observed at [NaCl 140 mM] in the plants of the *Mongal* variety inoculated with *R. fasciculatus* (43.95%), followed by that of the plants of the *Lady Nema* variety inoculated with *F. mosseae* (35.62%). In addition, plants of the *Mongal* variety, inoculated with *F. mosseae*, recorded the lowest dependency value (−131%). Plants of the *Lady Nema* variety, inoculated with *R. fasciculatus*, were the least dependent on mycorrhization with dependencies of −48.05%, 3.48%, −43.09% and −42.17%, respectively at [0, 70, 140 and 210 mM of NaCl].

3.2. Influence of Mycorrhizal Inoculation on the Agro-Morphological Parameters of Plants Grown under Salt Stress

3.2.1. Effect of Mycorrhizal Inoculation on the Survival Rate of Plants Grown under Increasing [NaCl]

The statistical analyzes revealed a significant [NaCl] × AMF Strain × Variety interaction ($F = 1.896$; $P = 1.02 \times 10^{-2}$). Indeed, the survival rate of plants, inoculated or not, decreased significantly with the increase in NaCl concentrations (*Lady Nema*: $F = 30.95$; $P = 2.51 \times 10^{-13}$; *Mongal*: $F = 61.07$; $P < 2 \times 10^{-16}$; Figure 5).

However, the variation in the decrease of the survival rates is not very different from one variety to another. Indeed, the smallest decrease (59%) is recorded at the level of plants of the *Lady Nema* variety inoculated with *C. etunicatum* and at the level of those of the *Mongal* variety inoculated with *R. fasciculatus*. Moreover, the greatest decrease is recorded with the control plants (91%) of the two varieties and those inoculated with *F. mosseae* (*Lady Nema* = 68% and *Mongal* =

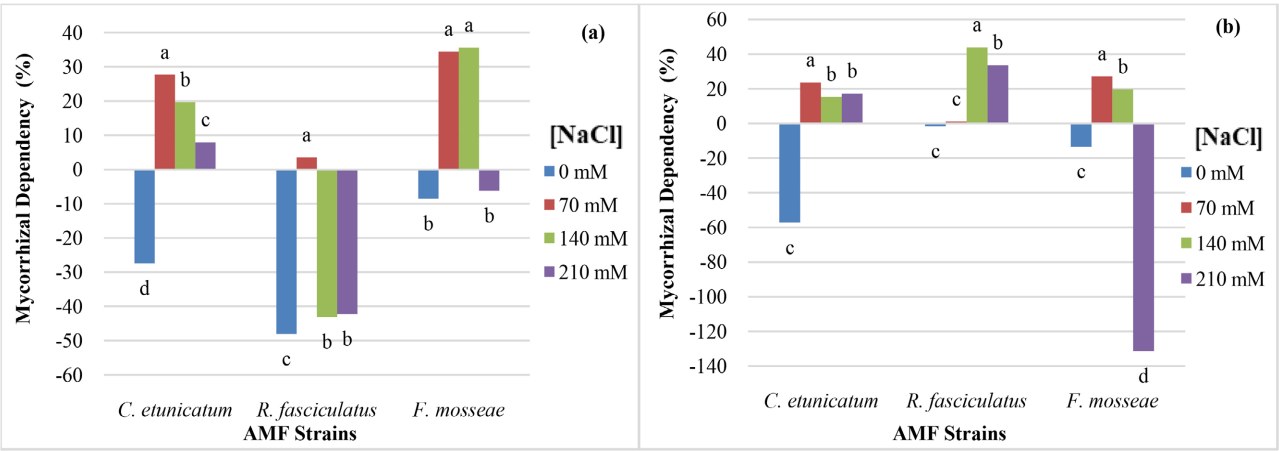

Figure 4. Effect of AMF strains on the relative mycorrhizal dependency of plants of *Lady Nema* (a) and *Mongal* (b) varieties grown under increasing [NaCl]. For each inoculation condition, the letters a, b, c and d designate homogeneous groups for the comparison of the means according to the Newman-Keuls test at the 5% threshold.

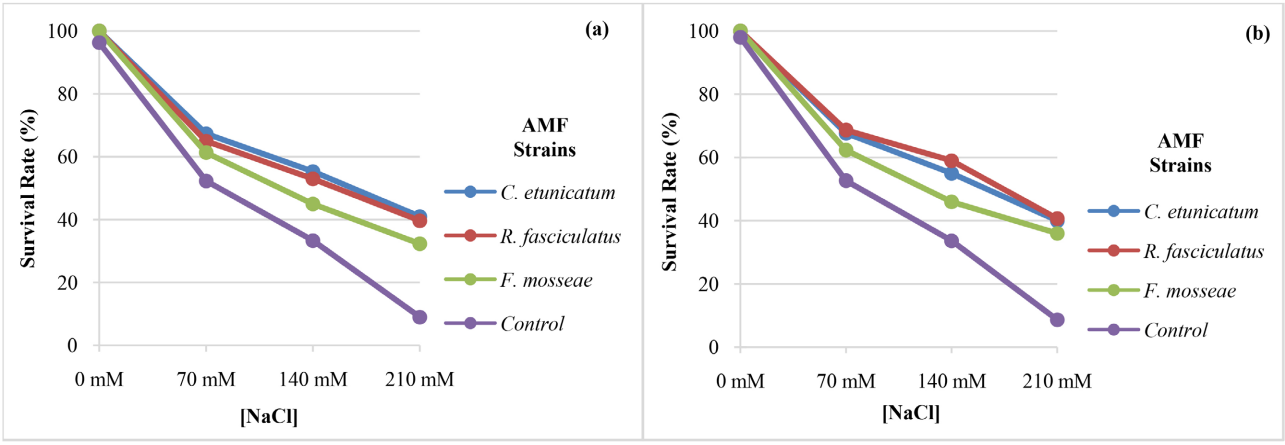

Figure 5. Effect of AMF strains on the evolution of the survival rate of plants of *Lady Nema* (a) and *Mongal* (b) varieties grown under increasing [NaCl].

64%). An improvement in survival rates compared to controls was noted thanks to mycorrhization. Indeed, at the level of the *Lady Nema* variety, improvements of 26%, 37% and 40% were recorded, respectively with the inoculation of *F. mosseae*, *R. fasciculatus* and *C. etunicatum*. Regarding the *Mongal* variety, the improvements observed are 27%, 39% and 43%, respectively with *F. mosseae*, *C. etunicatum* and *R. fasciculatus*. Thus, with regard to the *Lady Nema* variety, the plants inoculated with *C. etunicatum* recorded the highest survival rates with 100%, 67%, 55% and 41%, respectively at [0, 70, 140 and 210 mM of NaCl]. Regarding the *Mongal* variety, the plants inoculated with *R. fasciculatus* recorded the best survival rates with 100%, 69%, 59% and 41%, respectively at [0, 70, 140 and 210 mM of NaCl].

3.2.2. Effect of Mycorrhizal Inoculation on the Fresh and Dry Weight of the Aerial and Root Parts of Plants Grown under Increasing [NaCl]

The analysis of variance revealed a significant interaction [NaCl] × AMF strain × Variety concerning the fresh and dry weights of the aerial part (Fresh weight: $F = 34.02$; $P = 2 \times 10^{-16}$; Dry weight: $F = 4.223$; $P = 2.55 \times 10^{-4}$), those of the root part (Fresh weight: $F = 10.602$; $P = 7.46 \times 10^{-10}$; Dry weight: $F = 2.712$; $P = 9.67 \times 10^{-3}$) and as well as those of the total dry weight of the plants ($F = 4.653$; $P = 9.35 \times 10^{-5}$). These weights varied significantly with increasing NaCl concentrations for the two varieties (Table 4).

Salt stress significantly decreased dry weights. However, improvements of 99% at [NaCl 70 mM] and 6% at [NaCl 140 mM] in root dry weight of plants of the *Lady Nema* variety inoculated with *C. etunicatum* were observed. Inoculation with *R. fasciculatus* resulted in a 123% improvement in this weight. Regarding the *Mongal* variety, a 69% improvement in root dry weight is observed at [NaCl 70 mM] for plants inoculated with *C. etunicatum*. The greatest weights are obtained by inoculation with *C. etunicatum* for plants of the *Lady Nema* variety and with *R. fasciculatus* for those of the *Mongal* variety. Aerial dry weights were greater than root dry weights under all conditions for both varieties. In addition,

Table 4. Comparison of the means of the fresh and dry weights of the aerial and root parts of the plants as a function of the NaCl concentrations and of the AMF strains in the *Lady Nema* and *Mongal* varieties.

Varieties	AMF Strains	[NaCl] (mM)	AFW (g)	RFW (g)	ADW (g)	RDW (g)	TDW (g)	(ADW/TDW) × 100	(RDW/TDW) × 100	red/inc Rate ADW (%)	red/inc Rate RDW (%)
Lady Nema	*Claroideoglomus etunicatum*	0	**17.11a**	1.41b	**3.62a**	0.47b	**4.09a**	**88**	12		
		70	**16.32a**	**2.09a**	3.02b	**0.94a**	3.96b	76	**24**	**−16**	**+99**
		140	11.36b	1.50b	2.03c	0.50b	2.53c	80	20	−44	+6
		210	8.12c	0.84c	1.37d	0.24c	1.61d	85	15	−62	−50
	Rhizophagus fasciculatus	0	**16.88a**	1.82b	**3.08a**	0.44b	**3.52a**	87	13		
		70	14.06b	**3.20a**	1.98b	**0.99a**	2.97b	67	**33**	**−36**	**+123**
		140	8.70c	0.93c	1.05c	0.37b	1.42c	74	26	−66	−16
		210	5.39d	0.37d	0.86c	0.19c	1.04c	**82**	18	−72	−58
	Funneliformis mosseae	0	**12.52a**	**4.10a**	**2.59a**	**2.22a**	**4.80a**	54	46		
		70	**12.10a**	3.20b	**2.69a**	**1.68ab**	**4.37a**	62	38	**+4**	**−24**
		140	10.56b	2.41c	1.75b	1.42bc	3.16b	55	45	−32	−36
		210	7.35c	1.35d	0.44c	0.95c	1.40c	32	**68**	−83	−57
	Control	0	**15.80a**	**3.10a**	**3.34a**	**1.87a**	**5.21a**	64	**36**		
		70	**14.91a**	1.65b	2.05b	0.81b	2.86b	**72**	28	**−39**	**−57**
		140	10.72b	1.40b	1.41c	0.63c	2.04b	69	31	−58	−66
		210	2.14c	0.80c	1.03c	0.45d	1.48c	69	31	−69	−76
Mongal	*Claroideoglomus etunicatum*	0	**10.91a**	2.42b	**2.12a**	0.83b	**2.95a**	72	28		
		70	8.45b	**3.40a**	**1.94a**	**1.41a**	**3.34a**	58	**42**	**−9**	**+69**
		140	7.46c	1.70c	**1.66a**	0.57c	2.23b	75	25	−22	−32
		210	7.61c	0.99d	1.14b	0.35c	1.49c	**77**	23	−46	−58
	Rhizophagus fasciculatus	0	**17.04a**	**2.41a**	3.79a	**0.79a**	**4.57a**	**83**	17		
		70	15.61b	1.55bc	2.03bc	**0.56ab**	2.59c	78	22	−46	−29
		140	13.57c	**1.94ab**	2.58b	**0.79a**	3.37bc	77	**23**	**−32**	**0**
		210	9.54d	0.97c	1.54c	0.32b	1.86d	**83**	17	−59	−59
	Funneliformis mosseae	0	**11.69a**	**2.92a**	**2.96a**	**1.13a**	**4.10a**	**72**	28		
		70	10.66b	**3.33a**	**2.42a**	**1.09a**	3.51b	69	31	**−18**	**−4**
		140	8.54c	**2.94a**	1.64b	**0.71a**	2.35c	70	30	−45	−37
		210	5.12d	1.08b	0.29c	0.24b	0.53d	55	**45**	−90	−79
	Control	0	**14.44a**	**3.39a**	**3.19a**	**1.45a**	**4.64a**	69	**31**		
		70	10.70b	1.70b	1.95b	0.61b	2.56b	**76**	24	**−39**	**−58**
		140	9.01c	1.11bc	1.37bc	0.51bc	1.89c	73	27	−57	−65
		210	1.29d	0.66c	0.84c	0.39c	1.23d	68	32	−74	−73

AMF: Arbuscular Mycorrhizal Fungi; AFW: Aerial Fresh Weight, ADW: Aerial Dry Weight, RFW: Root Fresh Weight, RDW: Root Dry Weight, TDW: Total Dry Weight; red: reduction; inc: increase. For each variety, the values on the same column followed by the same letter are not significantly different according to Student-Newman-Keuls test at the 5% threshold.

inoculated plants recorded the highest weights compared to un-inoculated controls.

3.3. Influence of Mycorrhizal Inoculation on the Mineral Element and Proline Contents of Plants Grown under Salt Stress

3.3.1. Effect of Mycorrhizal Inoculation on the Mineral Element Content of the Leaves of Plants Grown under Increasing [NaCl]

The analysis of variance revealed a significant effect of the interaction [NaCl] × AMF strain × Variety concerning the contents of Potassium ($F = 74.46$; $P < 2 \times 10^{-16}$), Sodium ($F = 90.55$; $P < 2 \times 10^{-16}$) and Phosphorus ($F = 30.56$; $P < 2 \times 10^{-16}$). In fact, under all inoculation conditions, the leaf potassium and phosphorus contents of the plants of the two varieties decreased significantly with the increase in NaCl concentration, while those of sodium increased significantly ($P < 2 \times 10^{-16}$) (Table 5). In addition, the K^+ and P contents were higher for the inoculated plants compared to the non-inoculated controls. However, the opposite was noted with respect to Na^+ contents.

At [NaCl 210 mM], the potassium content decreased by more than 83% in plants of the *Mongal* variety inoculated with *F. mosseae* while the smallest decrease was obtained with the plants of the *Lady Nema* variety inoculated with *C. etunicatum* (67%). The sodium and phosphorus contents were higher for the plants of the *Mongal* variety inoculated with *C. etunicatum* (Na^+: 2213%; P: 85%), whereas they were lower for the plants of the *Lady Nema* variety inoculated with the same strain (Na^+: 1666%; P: 68%). Thus, for the *Lady Nema* variety, the plants inoculated with *C. etunicatum* recorded the highest potassium contents with 12.59, 12.7, 7.5 and 4.18 $mg \cdot g^{-1}$ of dry matter and phosphorus with 29.85, 23.86, 15.17 and 9.6 $mg \cdot g^{-1}$ of dry matter as well as the lowest sodium contents with 0.16, 1.08, 1.93 and 2.77 $mg \cdot g^{-1}$ of dry matter, respectively at [0, 70, 140 and 210 mM of NaCl]. For the *Mongal* variety, the plants inoculated with *R. fasciculatus* recorded the highest potassium content with 11.09, 9.04, 6.10 and 2.45 $mg \cdot g^{-1}$ of dry matter and phosphorus with 25.47, 18.70, 12.49 and 9.51 $mg \cdot g^{-1}$ of dry matter as well as the lowest sodium contents with 0.15, 1.23, 2.03 and 3.04 $mg \cdot g^{-1}$ of dry matter, respectively at [0, 70, 140 and 210 mM of NaCl].

3.3.2. Effect of Mycorrhizal Inoculation on the Mineral Element Content of the Roots of Plants Grown under Increasing [NaCl]

The statistical analyzes of the root K^+ and Na^+ contents as a function of increasing NaCl concentrations and AMF strains revealed a significant interaction [NaCl] × AMF strain × Variety (K^+: $F = 5.437$; $P = 48 \times 10^{-3}$; Na^+: $F = 29.83$; $P < 2 \times 10^{-16}$). Indeed, independently of the AMF strains, the K^+ content decreased with salinity (*Lady Nema*: $F = 109.434$; $P < 2 \times 10^{-16}$; *Mongal*: $F = 4.463$; $P = 5 \times 10^{-3}$) while that of Na^+ increased (*Lady Nema*: $F = 37.396$; $P < 2 \times 10^{-16}$; *Mongal*: $F = 38.127$; $P < 2 \times 10^{-16}$; Table 6). The best results were obtained with inoculated plants compared to non-inoculated control ones.

At [NaCl 210 mM], the greatest rate of decrease in K^+ content was obtained

Table 5. Effect of mycorrhizal inoculation on foliar K^+, Na^+ and P levels in plants of *Lady Nema* and *Mongal* varieties grown under increasing NaCl concentrations.

AMF Strains	[NaCl] (mM)	*Lady Nema*						*Mongal*					
		K^+ ($mg{\cdot}g^{-1}$ of dry matter)	Na^+ ($mg{\cdot}g^{-1}$ of dry matter)	P ($mg{\cdot}g^{-1}$ of dry matter)	Red/Inc Rate K^+	Red/Inc Rate Na^+	Red/Inc Rate P	K^+ ($mg{\cdot}g^{-1}$ of dry matter)	Na^+ ($mg{\cdot}g^{-1}$ of dry matter)	P ($mg{\cdot}g^{-1}$ of dry matter)	Red/Inc Rate K^+	Red/Inc Rate Na^+	Red/Inc Rate P
Claroideoglomus etunicatum	0	**12.59a**	0.16d	**29.85a**				**7.43a**	0.21d	**20.46a**			
	70	**12.7a**	1.08c	23.86b	**+1**	**+586**	**−20**	5.04b	1.53c	12.91b	**−32**	**+638**	**−37**
	140	7.5b	1.93b	15.17c	−40	+1131	−49	2.46c	3.27b	7.39c	−67	+1481	−64
	210	4.18c	**2.77a**	9.6d	−67	+1666	−68	1.30d	**4.79a**	3.12d	−82	+2213	−85
Rhizophagus fasciculatus	0	**8.30a**	0.17d	**20.86a**				**11.09a**	0.15d	**25.47a**			
	70	**7.57a**	1.4c	14.14b	**−9**	**+722**	**−32**	9.04b	1.23c	18.7b	**−18**	**+720**	**−27**
	140	3.46b	2.24b	8.17c	−58	+1219	−61	6.1c	2.03b	12.49c	−45	+1253	−51
	210	1.81c	**3.32a**	5.68d	−78	+1851	−73	2.45d	**3.04a**	9.51d	−78	+1927	−63
Funneliformis mosseae	0	**10.09a**	0.16d	**21.33a**				**6.1a**	0.23d	**13.17a**			
	70	8b	1.09c	16.56b	**−21**	**+583**	**−22**	5.24b	1.92c	8.86b	**−14**	**+723**	**−33**
	140	5.23c	1.99b	10.08c	−48	+1146	−53	2.43c	3.10b	5c	−60	+1232	−62
	210	2.36d	**3.02a**	6.01d	−77	+1788	−72	1.02d	**5a**	2.90d	−83	+2046	−78
Control	0	**7.36a**	0.19d	**15.18a**				**5.08a**	0.2d5	**12.22a**			
	70	4.79b	1.25c	12.47b	**−35**	**+546**	**−18**	3.81b	2.08c	7.99b	**−25**	**+733**	**−35**
	140	2.92c	2.50b	8.2c	−60	+1197	−46	1.11c	4.31b	4.53c	−78	+1625	−63
	210	0.9d	**4.30a**	5.21d	−88	+2130	−66	0.48d	**5.92a**	2.69d	−90	+2267	−78

AMF: Arbuscular Mycorrhizal Fungi; K^+: Potassium; Na^+: Sodium; P: Phosphorus; Red: Reduction; Inc: Increase. For each AMF strain, the values on the same column followed by the same letter are not significantly different according to the Student-Newman-Keuls test at the 5% threshold.

Table 6. Effect of mycorrhizal inoculation on root K^+ and Na^+ levels in plants of *Lady Nema* and *Mongal* varieties grown under increasing NaCl concentrations.

AMF Strains	[NaCl] (mM)	*Lady Nema*				*Mongal*			
		K^+ ($mg{\cdot}g^{-1}$ of dry matter)	Na^+ ($mg{\cdot}g^{-1}$ of dry matter)	Red/Incr Rate K^+	Red/Inc Rate Na^+	K^+ ($mg{\cdot}g^{-1}$ of dry matter)	Na^+ ($mg{\cdot}g^{-1}$ of dry matter)	Red/Inc Rate K^+	Red/Inc Rate Na^+
Claroideoglomus etunicatum	0	**10.03a**	0.19c			**5.26a**	0.35c		
	70	**9.56a**	**1.55a**	**−5**	+716	**5.55a**	**2.96a**	**+6**	+747
	140	4.40b	0.96b	−56	**+404**	1.18b	**2.88a**	−77	+723
	210	2.54c	1.04b	−75	+446	0.32c	2.14b	−94	**+511**
Rhizophagus fasciculatus	0	**6.51a**	0.26b			**9.33a**	0.24d		
	70	4.28b	**2.21a**	**−34**	**+750**	7.39b	**2.02a**	**−21**	+740
	140	2.04c	**2.27a**	−69	+773	3.09c	1.53b	−67	+539
	210	0.87d	**2.40a**	−87	+821	1.55d	1c	−83	**+317**

Continued

Funneliformis mosseae	0	**7.93a**	0.4b			**4.34a**	0.39b		
	70	6.54b	**1.98a**	**−18**	**+399**	2.10b	**2.99a**	**−52**	+667
	140	4.13c	**1.98a**	−48	+401	1.22c	**2.90a**	−72	+643
	210	1.83d	**1.99a**	−77	+403	0.92c	2.56ab	79	**+556**
Control	0	**4.39a**	0.62b			**3.48a**	0.6b		
	70	3.10b	**2.38a**	**−29**	**+283**	1.89b	**3.84a**	**−46**	**+540**
	140	1.05c	**2.55a**	−76	+312	0.43bc	**4.29a**	−88	+615
	210	0.42c	**2.68a**	−90	+333	0.12c	**4.65a**	−97	+675

AMF: Arbuscular Mycorrhizal Fungi; K^+: Potassium; Na^+: Sodium; Red: Reduction; Inc: Increase. For each AMF strain, the values on the same column followed by the same letter are not significantly different according to the Student-Newman-Keuls test at the 5% threshold.

with the plants of the *Mongal* variety inoculated with *C. etunicatum* (94%) while the lowest was obtained for the plants of the *Lady Nema* variety (75%) inoculated with the same strain. Thus, the highest K^+ contents were recorded in plants of the *Lady Nema* variety inoculated with *C. etunicatum* with 10.03, 9.56, 4.40 and 2.54 $mg{\cdot}g^{-1}$ of dry matter, respectively at [0, 70, 140 and 210 mM of NaCl]. Under these same salinity conditions, for the *Mongal* variety, the highest K^+ contents were recorded in plants inoculated with *R. fasciculatus*, with 9.33, 7.39, 3.09 and 1.55 $mg{\cdot}g^{-1}$ of dry matter.

At [NaCl 210 mM], for the *Lady Nema* variety, plants inoculated with *F. mosseae* revealed the lowest increase in Na^+ content (403%). In contrast, for the *Mongal* variety, inoculation with *R. fasciculatus* gave the lowest increase in Na^+ content (317%). Thus, for the *Lady Nema* variety, the lowest Na^+ contents were recorded on the plants inoculated with *C. etunicatum*, *i.e.*, 0.19, 1.55, 0.96 and 1.04 $mg{\cdot}g^{-1}$ of dry matter, respectively at [0, 70, 140 and 210 mM of NaCl]. Under these same salinity conditions, the lowest Na^+ contents, for the *Mongal* variety, were recorded with the inoculation of *R. fasciculatus* (0.24, 2.02, 1.53 and 1 $mg{\cdot}g^{-1}$ of dry matter).

3.3.3. Evolution of the K^+/Na^+ Selectivity Ratio in the Leaves and Roots of Plants Grown under Increasing [NaCl]

Increasing NaCl concentrations negatively impacted the K^+/Na^+ selectivity ratio with drastic decrease rates (Table 7). This ratio is greater at the level of the leaves compared to the roots. However, at [140 and 210 mM of NaCl], this ratio was greater at the level of the roots of plants of the *Lady Nema* variety inoculated with *C. etunicatum*. For the *Mongal* variety, this ratio was in favor of the roots in plants inoculated with *R. fasciculatus* at [NaCl 210 mM l]. For the *Lady Nema* variety, the highest selectivity ratios were recorded in plants inoculated with *C. etunicatum* (Leaves: 80.17, 11.79, 3.88 and 1.51; Roots: 52.77, 6, 17, 4.60 and 2.45 respectively at [0, 70, 140 and 210 mM of NaCl]). However, at [NaCl 210 mM], the rate of decrease in this ratio at the leaf level was between 98.12% (*C. etunicatum*)

Table 7. K^+/Na^+ ratio in leaves and roots as a function of NaCl concentration and AMF strains in plants of *Lady Nema* and *Mongal* varieties.

AMF Strains	[NaCl] (mM)	*Lady Nema*		*Mongal*	
		Leaves	Roots	Leaves	Roots
		K^+/Na^+	K^+/Na^+	K^+/Na^+	K^+/Na^+
Claroideoglomus etunicatum	0	**80.17**	**52.77**	**35.89**	**15.02**
	70	**11.79**	6.17	3.30	1.87
	140	3.88	4.60	0.75	0.41
	210	1.51	2.45	0.27	0.15
Rhizophagus fasciculatus	0	**48.84**	**25.03**	**73.91**	**38.88**
	70	5.42	1.94	**7.35**	3.67
	140	1.54	0.90	3.00	2.02
	210	0.54	0.36	0.81	1.55
Funneliformis mosseae	0	**63.08**	**20.02**	**26.18**	**11.13**
	70	**7.32**	3.31	2.73	0.70
	140	2.62	2.08	0.78	0.42
	210	0.78	0.92	0.20	0.36
Control	0	**38.15**	**7.08**	**20.32**	**5.81**
	70	3.84	1.31	1.83	0.49
	140	1.17	0.41	0.26	0.10
	210	0.21	0.16	0.08	0.03

AMF: Arbuscular Mycorrhizal Fungi; K^+: Potassium; Na^+: Sodium.

and 99.45% (control). On the other hand, at the root level, it was between 95.36% (*C. etunicatum*) and 98.54% (*R. fasciculatus*).

For the *Mongal* variety, the highest selectivity ratios were obtained from plants inoculated with *R. fasciculatus* (Leaves: 73.91, 7.35, 3 and 0.81; Roots: 38.88, 3.67, 2.02 and 1.55 respectively at [0, 70, 140 and 210 mM of NaCl]). The reduction rate of this ratio at the level of the leaves at [NaCl 210 mM] was between 98.91% (*R. fasciculatus*) and 99.60% (control) while at the level of the roots, it was between 96.02% (*R. fasciculatus*) and 99.56% (control).

3.3.4. Influence of Mycorrhizal Inoculation on the Proline Contents of Plants Grown under Increasing [NaCl]

The analysis of variance of the effect of mycorrhization on the proline content, determined at the level of the aerial part of the plants subjected to increasing concentrations of NaCl, revealed that the interaction [NaCl] × Strain of AMF × Variety is very significant ($F = 3.134$; $P = 3.46 \times 10^{-4}$; **Figure 6**). Indeed, the proline content of the plants increased significantly at all inoculation conditions with the increase in NaCl concentration (*Lady Nema*: $F = 499$; $P < 2 \times 10^{-16}$; *Mongal*: $F = 324, 1$; $P < 2 \times 10^{-16}$).

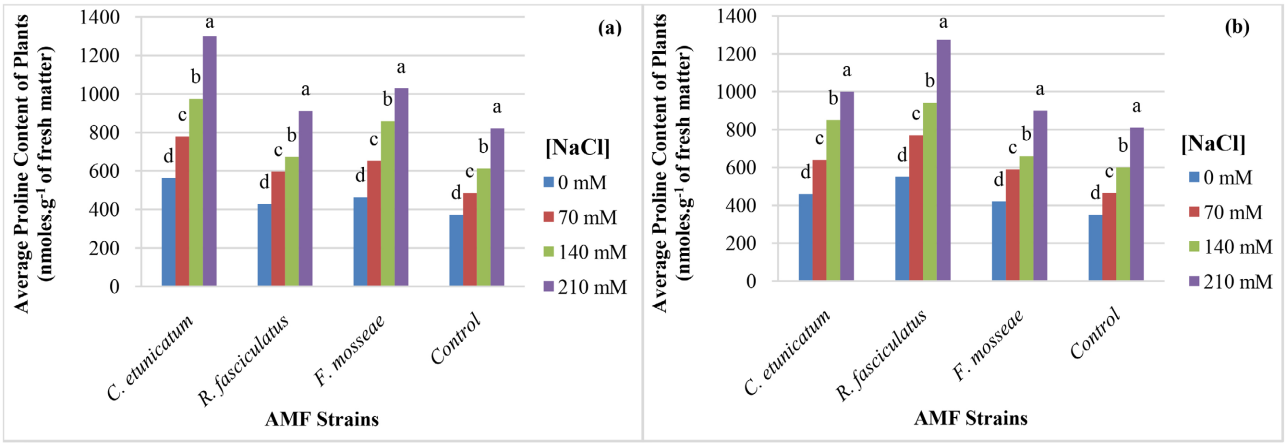

Figure 6. Effect of AMF strains on the average proline content of plants of *Lady Nema* (a) and *Mongal* (b) varieties grown under increasing [NaCl]. For each inoculation condition, the letters a, b, c and d designate homogeneous groups for the comparison of the means according to the Newman-Keuls test at the 5% threshold.

Regarding the *Lady Nema* variety, this increase was more significant in plants inoculated with *C. etunicatum* (131%) while it was lower in plants inoculated with *R. fasciculatus* (113%). For the *Mongal* variety, the highest increase was obtained with the inoculation of *R. fasciculatus* (132%) and the lowest with the inoculation of *F. mosseae* (114%). However, the inoculated plants recorded higher proline contents than the controls. Thus, the plants inoculated with *C. etunicatum* obtained the best proline contents with 537, 779, 975 and 1300 nmoles·g^{-1} of fresh matter, respectively at [0, 70, 140 and 210 mM of NaCl] for the plants of the *Lady Nema* variety. Under the same salinity conditions, for the *Mongal* variety, the best proline contents were obtained on plants inoculated with *R. fasciculatus*, with 550, 770, 942 and 1275 nmoles·g^{-1} of fresh material. Plants of the *Lady Nema* variety recorded higher proline contents than those of the *Mongal* variety.

4. Discussion

4.1. Influence of Mycorrhization on Tomato Plants Subjected to Salt Stress

In semi-arid regions, mycorrhizal symbiosis plays a major role in the development of crops and their tolerance to abiotic stresses, particularly for tomatoes. AMF have been associated with a wide range of plants and different soil salinity levels [1] [7]. Indeed, AMF have the ability to associate with the roots of plants, thereby improving their hydromineral nutrition [10]. There are two ways of root colonization of a plant by an AMF. Primary colonization from pre-symbiotic fungal hyphae from a spore and secondary colonization from the extra-root mycelium of a fungus that has already colonized the root system of a host plant. Once the hyphae are in the root cells, they differentiate into highly branched arbuscules occupying most of the cell volume and forming an extensive surface for nutrient exchanges [25]. They also grow out of the root forming a branching mycelium that explores the soil for the absorption of mineral nutrients and wa-

ter. However, high salt levels in soil can reduce the colonization capacity and germination of AMF spores [7].

According to the present study, the frequencies and intensities of mycorrhization, as well as the relative mycorrhizal dependency varied significantly ($P < 2 \times 10^{-16}$) with increasing NaCl concentrations. The decrease in the frequency of mycorrhization varies from 86% to 92% and that of the intensity of mycorrhization from 75% to 93% at [NaCl 210 mM]. A decrease in root infection by AMF of 51% was recorded in tomatoes grown under saline conditions (7500 ppm) [8]. Plants inoculated with *C. etunicatum* and *R. fasciculatus* revealed the best frequencies and intensities of mycorrhization in *Lady Nema* and *Mongal* varieties, respectively. These mycorrhization parameters are more considerable with the plants of the *Lady Nema* variety compared to those of the *Mongal* variety. Indeed, plants of the *Lady Nema* variety inoculated with *C. etunicatum* recorded mycorrhization frequencies of 94.03%, 94.01%, 54.01% and 13.05% and those of the *Mongal* variety inoculated with the *R. fasciculatus* strain recorded 90.24%, 91.69%, 50.36% and 10.86%, respectively at [0, 70, 140 and 210 mM of NaCl]. Plants of the *Lady Nema* variety inoculated with *C. etunicatum* also recorded the best mycorrhization intensities with 39.59%, 40.47%, 21.33% and 9.92% while those of the *Mongal* variety inoculated with the *R. fasciculatus* strain obtained mycorrhization intensities of 35.82%, 35.14%, 14.86% and 5.71% in the same saline conditions. However, a lower reduction of 14% and 27% in the frequency of mycorrhization in tomato inoculated with *F. mosseae*, is noted respectively under medium (4.7 $dS \cdot m^{-1}$) and high salt stress (7.4 $dS \cdot m^{-1}$) [10]. Small reductions in the frequency of mycorrhization (*Funneliformis mosseae*) of 24.6% and 21.9% at 4.9 $dS \cdot m^{-1}$ and 35% and 41% at 7.1 $dS \cdot m^{-1}$ were obtained, respectively in two tomato varieties *Pello* (tolerant) and *Marriha* (susceptible) [6]. Mycorrhization frequencies twice lower than those recorded in our study (control: 55% and at [NaCl 100 mM]: 27%) were also observed in tomato plants inoculated with *Funneliformis mosseae* [11]. Degrees of relative mycorrhizal dependency are classified as follows: excessive (RMD > 75%), high (50 < RMD < 75%), medium (25 < RMD < 50%), marginal (RMD < 25%), and independent (RMD ≤ 0%) [26]. The mycorrhizal dependencies recorded in our experiments show positive and negative values relating to biomass gains or losses in mycorrhizal plants. However, without saline constraint, the dependencies are all negative at all inoculation conditions, *i.e.*, the plants are independent of mycorrhization. In addition, the maximum dependency is observed at [NaC140 mM l] in plants of the *Mongal* variety inoculated with *R. fasciculatus* (43.95%), followed by those of the *Lady Nema* variety inoculated with *F. mosseae* (35.62%). Thus, in the presence of saline constraint, the RMD is accentuated because the plants of the two varieties need more and more to associate with the AMF which results in an average dependency. However, plants of the *Lady Nema* variety inoculated with *R. fasciculatus* at [140 and 210 mM of NaCl] recorded RMDs of −43.09% and −42.17%, respectively. In addition, those inoculated with *F. mosseae* at [NaCl 210 mM]

also recorded a RMD of −6.21%. Thus, with these RMD less than 0, these plants always remain indifferent to mycorrhization. In the *Mongal* variety, plants inoculated with *F. mosseae* at [NaCl 210 mM] are also indifferent to mycorrhization with a RMD of −131.25%. Mycorrhizal dependency (MD) expresses the contribution of AMF in stimulating plant growth compared to the same non-mycorrhizal plants. Mycotrophic plants such as tomato have a coarse root system which determines their reliance on symbiosis [12]. Some species such as carrot and onion have a strong mycorrhizal dependency, while others such as sorghum and maize have an intermediate mycorrhizal dependency. Finally, a last category including wheat, rice and tomato show a low dependency on mycorrhizal colonization [27]. This is in contradiction with our results which revealed an intermediate mycorrhizal dependency of the tomato varieties studied. For a given soil and plant, there is a maximum quantity of extractable phosphorus above which the response of the plant to mycorrhization is zero, at least as far as plant growth is concerned [28]. Several factors can influence the MD of the plants, including the plant species used, the structure of the root system, the fungal symbiont and the content of the soil in assimilable phosphorus. Under unfavorable mineral nutrition conditions, the two partners in the symbiosis can compete for carbonaceous substrates, resulting in a depressive effect of the fungus on the juvenile growth of plants [5].

The plant factors that are at the origin of the differences observed in the aptitude for endomycorrhizal colonization seem to be linked to the morphological and physiological characteristics of the plants [12]. Our results showed that tomato still had the ability to establish symbiotic relationships with AMF even under high saline concentration. A similar conclusion was made by [29]. Several authors have also shown that salinity reduces mycorrhizal colonization by inhibiting spore germination and hyphal growth or by reducing the spread of mycorrhizal colonization and the number of arbuscules [30]. The negative effect of soil salinity on mycorrhizal root infection could also be due to the accumulation of H_2O_2 in the roots of mycorrhizal plants, which could induce the degradation of arbuscules [31].

4.2. Influence of Mycorrhization on the Agro-Morphological Parameters of Tomato Plants Subjected to Salt Stress

The direct effects of soil salinity on plant growth may involve three distinct physiological pathways: firstly, plants subject to the low osmotic potentials of saline soil are at risk of physiological drought because they must maintain lower internal osmotic potentials to prevent water movement from roots to soil [3]. Secondly, the toxic effects of specific ions such as Na^+ and Cl^-, disseminated in saline soils, disrupt the structure of enzymes and therefore their function, damage cellular organelles and disrupt photosynthesis, respiration and protein synthesis [32]. Finally, salinity also leads to a nutrient imbalance in the plant caused by a change in the absorption and/or transport of nutrients to the aerial part, which leads to ionic deficiencies [33]. The application of AMF could improve the phy-

sico-chemical and biological characteristics of the soil [34]. Furthermore, the spread of AMF hyphae beyond the root zone provides the nutrients necessary for plant development [25]. Thus, several studies have demonstrated that several species of AMF are involved in promoting plant resistance to salinity [31]. Our results revealed a significant decrease ($P < 2 \times 10^{-16}$) in survival rates which increases with high NaCl levels and treatment duration with better results in inoculated plants compared to controls. Several authors have reported that inoculated plants grow better than un-inoculated ones under salt stress [32]. Thus, the survival rate of the plants in this study is greater (>40%) on the plants inoculated with *C. etunicatum* for the *Lady Nema* variety and *R. fasciculatus* for the *Mongal* variety. A one hundred percent survival rate is obtained in a variety of tomato inoculated with *F. mosseae* in a salt stress situation (ECse = 7 $dS{\cdot}m^{-1}$) [29]. The effects of salinity observed would result from a disturbance of the water and nutrient supply as well as toxicity following a strong accumulation of salt in the leaves [35]. Indeed, following an increase in the osmotic potential in the culture substrate, the cell turgor would be based on the accumulation of ions in the vacuole, which alters the cell organelles causing the appearance of leaf necrosis and, finally, the death of the cell plant. To adapt to salt stress, the plant can avoid damage by reducing growth [33]; this is the most common effect of abiotic stresses on plant physiology. Indeed, this delay in development allows the plant to accumulate energy and resources to combat stress before the imbalance between the interior and exterior of the organism increases to a threshold where the damage will be irreversible [35]. Plant protection by mycorrhization against salt stress has also been reported to result from increased and/or better selection in nutrient uptake, accumulation of osmoregulatory compounds, high stomatal conductance, an increase in photosynthetic activity or even a limitation of leaf dehydration [33].

The negative impact of salinity on plant development is reflected in the fresh and dry weight of plants [30]. Thus, in the present study, a clear and significant decrease in the fresh and dry weight of the aerial and root parts is observed with the increase in NaCl content. However, the inoculated plants showed better development compared to the non-inoculated ones. Indeed, an increase in fresh root weight is observed at [NaCl 70 mM] varieties for plants inoculated with *R. fasciculatus* (76% for *Lady Nema*) and *C. etunicatum* (48% and 41% respectively for *Lady Nema* and *Mongal* varieties. At [NaCl 70 mM], the dry weight of plants of the *Lady Nema* variety increased by 99% (*C. etunicatum*) and 123% (*R. fasciculatus*) while that of the plants of the *Mongal* variety increased by 99% (*C. etunicatum*). Similar results under saline conditions were obtained in tomato plants inoculated with *F. mosseae* [36] and with different AMF strains including *R. fasciculatus* and *F. mosseae* [29]. Several other authors have reported the beneficial effect of AMF on the dry weight of plants under osmotic and ionic stress conditions [30]. Maintaining water homeostasis is essential to mitigate the impact of salinity on plant growth and crop production. Under stress conditions, inocula-

tion with AMF often improves the water status of plants due to the presence of extra root hyphae which absorb more water. AMF colonization increases active solute transport as a mechanism that allows water to continue to flow through plant roots [37]. However, a reduction in the aerial dry weight of 62% to 83% and in the root dry weight of 50% to 58% in the presence of [NaCl 210 mM] is observed on the mycorrhizal plants of the *Lady Nema* variety compared to non-stressed plants. With regard to the *Mongal* variety, the reduction in aerial dry weight varies between 46% and 90% and that of root dry weight between 58% and 79%, always in the presence of [NaCl 210 mM]. Reductions in aerial (50%) and root (60%) dry weights were observed in tomatoes under salt stress conditions [38]. However, the aerial dry weights are greater than those of the roots in all conditions for both varieties, which suggest that the AMF would promote better development of the aerial part *versus* the root part and that salinity has a greater impact on this root part which is the part in direct contact with harmful ions. Reduced plant growth under saline stress is attributed to reduced water and nutrient availability due to excessive NaCl levels in the growth medium, but also by imbalance and specific ion toxicity leading to down-regulation of other metabolic activities [39]. The reduction in biomass can be caused by several modifications, the main ones being: 1) reduction in the thickness of the epidermis, mesophyll, intercellular spaces and reduction in cell size [40]; 2) reduction in the number of chloroplasts, leaf area, and stomatal density [41]; 3) structural damage to cell walls, dilation and reduction in the number of mitochondrial ridges; 4) damage caused by stress-induced increase in ethylene [42]. It may also be due to ionic toxicity caused by the accumulation of Na^+ and Cl^- ions [32]. The heterogeneity of the results with the different AMF strains could be explained by the fact that the AMF diverge functionally [15]; different species show heterogeneity in performance in hyphal growth, fungal uptake and symbiotic nutrient transport [5].

4.3. Influence of Mycorrhization on the Mineral Element Contents of Tomato Plants Subjected to Salt Stress

The effectiveness of a plant in controlling the consumption, distribution and compartmentalization of Na^+ is decisive for its tolerance to salinity [4]. Soil salinity significantly reduces the concentration of beneficial elements making it difficult for nutrients such as P and K^+ to be absorbed [39]. This leads to nutritional disorders that AMF could improve [37].

Under our experimental conditions, the mineral nutrition of tomato plants was found to be dependent on the variety, the strain of mycorrhizal fungus inoculated and also on the level of salinity applied. Indeed, with regard to the two varieties tested, the foliar contents of potassium and phosphorus decreased with salinity while that of sodium increased. Similar results were obtained on several tomato genotypes [38]. At the root level, the K^+ content decreased with salinity while the Na^+ content increased significantly. The inoculated plants garner higher

K^+ and P contents than those recorded on the non-inoculated plants. In addition, Na^+ contents are higher in non-inoculated plants. Numerous studies have indicated that AMF contribute to plant growth via enhancing the uptake of mineral nutrients, especially immobile (P) ones from the soil [37]. This may be due to increased availability and/or transport (absorption/translocation) of these minerals by AMF hyphae. Mycorrhizal fungi have a regulatory effect on the translocation of Na^+ at the level of the aerial part, which makes it possible to maintain a lower Na^+ aerial part/root part ratio in the tissues of inoculated plants than in the tissues of non-inoculated ones [7]. Regarding the potassium contents, they decreased by more than 65% at [NaCl 210 mM] for the *Lady Nema* and *Mongal* varieties. The best results are obtained with the inoculation of *C. etunicatum* in the plants of the *Lady Nema* variety, followed by the inoculation with *R. fasciculatus* in the plants of the *Mongal* variety. Tomato plants inoculated with *Glomus intraradices* (*Rhizophagus intraradices*) obtained a 90% reduction in K^+ levels [2]. These results are similar to the values obtained in our work. However, the increase in Na^+ contents (200%) is far lower than that obtained in our work. As for mycorrhizal tomato plants with *F. mosseae* and grown under saline stress, a greater drop in phosphorus and potassium levels (+86%) was recorded [6]. However, the increase in sodium of those (155% to 249%) is far less significant than that obtained in our experiments. We noted a positive correlation between leaf potassium and phosphorus contents, but also a negative correlation between potassium, phosphorus, and sodium contents. Similar results were obtained in tomato plants mycorrhized with *F. mosseae* [10]. At the root level, a high K^+ content is accompanied by a low Na^+ content and *vice versa*. Similar results in a salinity situation were also reported for tomato plants inoculated with *R. intraradices* [2]. Increasing NaCl concentrations also negatively impacted the K^+/Na^+ selectivity ratio with drastic decrease rates. However, this ratio is greater at the level of the leaves compared to the roots. Meanwhile, at [140 and 210 mM of NaCl], this ratio is greater at the level of the roots of plants of the *Lady Nema* variety inoculated with *C. etunicatum*. For the *Mongal* variety, this ratio is in favor of the roots for the plants inoculated with *R. fasciculatus* at [NaCl 210 mM]. This testifies to the respective effects of these AMF in mineral nutrition by promoting significant absorption of K^+. Therefore, higher values of these ratios protect photosynthetic tissues by suppressing Na^+ influx and improving hydraulic conductivity and cell signaling pathway [43]. It could also be attributed to the enhancement of the affinity of K^+ transporters or to the regulation of K^+, Na^+ transporters and H^+ pumps, which generate the force necessary to transport these elements under saline conditions [40]. Under salt stress, AM symbiosis can increase K^+ uptake and reduce Na^+ translocation to stems and leaves [36]. The importance of maintaining appropriate K^+/Na^+ ratios for metabolic functioning has become widely accepted as an indicator of NaCl sensitivity [44]. In a study carried out on 60 species, including the tomato, it was reported that AMF could induce a marked increase in leaf K^+/Na^+ ratio by 28% and root

ratio by 115% [45]. They also recorded a small increase in Na^+ (roots) and K^+ (leaves) content of 18%. AMF vesicle vacuoles can store different ions such as sodium and chloride under salt stress [46. In our studies, AMF influenced the increase in potassium and phosphorus levels more than the reduction in sodium levels. In addition to balancing the quantities of Na^+ and Cl^- by storing them in their vacuole [46], AMF induce an increase in K^+ contents which also contribute to greater root hydraulic conductivity and consequently an improvement in water availability under osmotic stress [37]. Under normal conditions, plant cytosol contains high concentrations of K^+ and low concentrations of Na^+, which imparts a negative electrical potential to cells [47]. At high salt concentrations, there could be a competition between Na^+ and K^+ ions for the occupation of entry sites in the root plasma membrane which affects K^+-dependent metabolic processes and also disrupts the integrity of root membranes [7]. Thus, membrane transporters exhibit low affinity to K^+ and high affinity to Na^+ from the environment outside the cytosol. The potassium ion is vital for the plant, as it is necessary for osmotic balance, plays a role in the opening and closing of stomata and is a key factor in protein biosynthesis [37]. The impact of mycorrhizal symbiosis on potassium uptake demonstrated that its accumulation in plants was linked to an improvement in their tolerance to salinity [37]. Unlike many other mineral nutrients, phosphorus is very poorly mobile in soils. Under the action of root removal, areas of impoverishment are quickly created around the roots. A small proportion (generally less than 1%) is immediately available to plants, which have difficulty acquiring this element when their needs are great [48]. Indeed, phosphorus is an essential element for the life of the plant. This compound enters into the synthesis of many molecules such as ATP, monophosphate nucleotides, phospholipids and certain enzymes and co-enzymes [49]. Thus, plants have developed various strategies to increase their ability to absorb phosphorus or its availability in soils [26]. Alongside the strategies allowing the plant to directly take up phosphorus from the soil, the most common method of taking up phosphorus consists of the so-called "mycorrhizal" route, *via* the extra-root mycelium of the AMF [48]. To access soil phosphorus pools inaccessible to plants, AMF would be able to hydrolyze organic phosphorus into inorganic phosphorus to make it available in the soil to the plant or even transfer it directly to the host plant [3] in exchange for carbohydrates from the plant and transferred to the MAC through the mycorrhizal interface [25]. The reduction in phosphorus uptake in saline soils has been attributed to the precipitation of $H_2PO_4^-$ with Ca^{2+} ions in the soil [26]. Studies have revealed that the symbiosis of plants with arbuscular fungi induces the expression of specific P transporters [50].

4.4. Influence of Mycorrhization on the Proline Contents of Tomato Plants Subjected to Salt Stress

Salinity decreases the osmotic potential of the soil solution and therefore reduces water uptake by the roots. Cellular turgidity is reduced which leads to a pheno-

menon of plasmolysis. Some plants regulate their internal osmotic pressure by synthesizing osmoprotectors, mainly amino acids such as proline. When present in high concentrations, organic solutes are called "osmolytes" because they maintain high osmotic pressure for important osmotic functions. This term is synonymous with the term "compatible solutes", because they are compatible with enzymatic activities. The level of proline is determined by the balance between its biosynthesis and its catabolism [51]. Proline synthesis is an adaptive action taken by plants and its content is correlated with tolerance to harmful salts [52]. Indeed, a significant increase ($P < 2 \times 10^{-16}$) in the proline content of the plants is observed at all the inoculation conditions with the increase in the NaCl concentration. The inoculated plants stored higher levels of proline than the un-inoculated ones. Thus, for the *Lady Nema* variety, plants inoculated with *C. etunicatum* have the highest increase in proline content (131%). For the *Mongal* variety, inoculation with *R. fasciculatus* gave the greatest increase (132%). Several authors have recorded a significant increase in proline content of up to 500% in tomato plants inoculated with AMF [8]. In this present study, under salt stress conditions, tomato plants recorded increased proline levels, which were significantly increased by the application of AMF. Studies have also revealed an increase in proline levels in tomato plants grown under saline conditions thanks to inoculation with *F. mosseae* [10]. Increasing proline levels may be a defensive response to improve plant tolerance to salt stress by maintaining osmotic balance [52] and mitigating free radical damage [31]. In the presence of NaCl, the colonization of the roots by AMF could set up mechanisms allowing the launching of a better synthesis of proline and, therefore, a better tolerance of the plant to salt stress [39]. Proline plays several major roles during saline stress. It acts as a metal chelator, a signaling molecule, an active anti-oxidant and a defense molecule that helps buffer cellular redox potential and scavenges free radicals [51]. An increase in the proline of tissues has also been considered an incidental consequence of NaCl exposure in less tolerant plants [44].

5. Conclusion

The study of the growth and development of tomato plants (*Solanum lycopersicum* L.) of the *Mongal* and *Lady Nema* varieties inoculated with AMF and cultivated in soil with increasing concentrations of NaCl revealed a significant interaction between the varieties, AMF strains and salinity levels. The varietal response was dependent on AMF strain and soil NaCl concentration. The salt stress considerably reduced the growth of the physiological and biochemical characteristics of the plants for the two varieties. However, plants inoculated with AMF revealed significant improvement in growth and mycorrhization parameters despite the applied salt stress. Thus, the AMF allowed a better development of the aerial part and that of the roots of the plants with more consequent advantage of the aerial part. Similarly, the mycorrhizal plants considerably increased the phosphorus, potassium and proline contents while reducing those

of sodium. Thus, the *Lady Nema* variety appeared to be more tolerant to salinity thanks in particular to AMF with more effective adaptation mechanisms than those developed by the plants of the *Mongal* variety. Therefore, for the *Lady Nem*a variety, the association with *Claroideoglomus etunicatum* brought the best results, followed by that *Funneliformis mosse*ae and, finally, *Rhizophagus fasciculatus*. For the *Monga*l variety, the *Rhizophagus fasciculatus* strain is the best fungal partner, followed by *Claroideoglomus etunicatum* and *Funneliformis mosseae* for adaptation to salt stress conditions.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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