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Mycorrhizal Benefits of Salt-Stressed *Cinnamomum camphora* (L.) Presl. May Be Related to P and Mn^{2+} Contents in Shoots, Biomass Allocation, and K^+/Na^+ in Roots and Shoots

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Abstract: Arbuscular mycorrhizal fungi (AMF) are taken as bioameliorators to alleviate the detrimental effects of salt stress. However, how AMF affect the performance of *Cinnamomum camphora*, an economically important species, remains unclear. In this study, we evaluated the interactive effects of AMF and salinity on the growth, nutrient acquisition, and ion ratios of *C. camphora*. A factorial experiment was implemented in a greenhouse with four fungal regimes (inoculation with sterilized AMF, with *Funneliformis mosseae* or *Rhizophagus irregularis*, either alone or in combination), and three salt regimes (0, 50, and 200 mM NaCl). Results showed that salinity alone significantly reduced the total dry weight, mycorrhizal colonization, K^+ concentration, and ionic homeostasis (particularly K^+:Na^+, Mg^{2+}:Na^+, and Ca^{2+}:Na^+) of whole plants. Mycorrhizal inoculation, particularly with *R. irregularis*, strongly mitigated some of the detrimental effects of salinity, enhancing the salt tolerance of *C. camphora*. Furthermore, the host plants benefited from the presence of AMF, mainly because they enhanced P and Mn^{2+} concentrations in the shoots, adjusted biomass allocation, and shifted the selective transporting capacity of K^+ over Na^+ from roots to shoots. Our results suggested that building mycorrhizal association between *C. camphora* and *R. irregularis* may be useful for plant cultivation in coastal areas.

Keywords: salinity; *Cinnamomum camphora*; P and Mn^{2+} concentrations; K^+/Na^+; *Funneliformis mosseae*; *Rhizophagus irregularis*

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1. Introduction

The salinization of soil refers to increasing the salinity of soil to high levels (>40 mM or >0.1% soil content) and is an increasing environmental problem in agriculture, forestry, and environmental science [1–3]. The total area of salt-affected soil is estimated to cover 1 billion ha in more than 100 countries [4,5]. Furthermore, this area is increasing by 1.5 M ha per year, which will result in 50% land loss by 2050 [6]. Soil salinization is severely aggravated by irrigation with inadequate drainage facilities, erroneous fertilization, and salt-water intrusion [4,7]. Moreover, salinization causes serious soil degradation in coastal areas [8]. Consequently, this is a major problem in China, where the coastline extends up to 3.2×10^4 km, for both the mainland and islands combined [8]. Salinity negatively affects plant water potential and ionic balance through the compounding effects of osmotic stress, ion toxicity, and nutrient imbalance, all of which significantly reduce plant growth and productivity [7,9,10]. In addition to the adaptive mechanisms developed by plants, new biological approaches provide necessary and practical ways of improving plant tolerance to salinity. In particular, there is increasing scientific interest in the role of mycorrhizal symbiosis with respect to plant responses to environmental stresses [10–12].

Most terrestrial plants can form fungal symbioses, among which those involving arbuscular mycorrhizal (AM) fungi (AMF) are the most dominant types [13]. AMF can often be found in saline soils [9,14], even though salinity adversely affects the formation and function of AMF [15]. However, there is compelling evidence that mycorrhizal colonization of the roots improves salinity tolerance in both glycophytes and halophytes [1,12,16,17]. Actually, AM symbiosis is a complex biological interaction, and its impact widely varies under different saline scenarios and specific plant–AMF combinations [18,19]. In particular, some mycorrhizal benefits are attributed to the specific responses of the host plant species to mycorrhizal colonization [9], whereas others are induced by the properties of the colonizing fungus [20,21]. Therefore, it is important to determine the mechanisms that facilitate plant growth under saline conditions. Some physiological processes were identified as an underlying mechanism for the fungi-induced amelioration of salinity stress, including enhancing the acquisition of nutrients with low mobility (especially P), reducing Na^+ uptake and translocation, preserving ionic homeostasis, and changing the microbial community in the rhizosphere [9,10,12,22]. However, most studies on this subject have focused on herbaceous plants (72.4%) rather than woody perennial species (27.1%) [9]. Consequently, mycorrhizal effects on tree growth under saline conditions remain poorly understood.

Cinnamomum camphora (L.) Presl. (also known as the camphor tree) is a member of the Lauraceae family and an economically important indigenous tree species in China, Japan, Korea, and Vietnam [23]. This species has been cultivated in southern China for more than 2000 years and is widely used for ornamental purposes; producing furniture, perfume, and herbal medicine; and for soil restoration in coastal areas [24]. In recent decades, with the expansion of salt-water intrusion and exaggerated soil salinization in the coastal areas of southern China, high salinity tolerance is becoming a valuable characteristic for plants growing in these areas [8]. However, *C. camphora* only exhibits moderate salt tolerance, with a salinity threshold of 0.2% (100 mM NaCl) [25]. Furthermore, *C. camphora* is highly dependent on AMF (with root colonization up to 81.85%) [26]. Given that enhancing nutrient uptake is a prominent effect of AMF on plant performance under stressful conditions [9,13], we hypothesized that pre-inoculating this plant with AMF may alleviate the detrimental effects of salinity stress through nutrient enhancement. Furthermore, because mycorrhizal efficiency is usually stress-dependent, and various fungal species can differently regulate plant response to salinity [2,18], we also hypothesized that salt tolerance conferred by AMF may vary with the intensity of salt stress and fungal isolates. To test the hypotheses, we implemented a full factorial experiment to determine the effect of an established mycorrhizal association on the growth, nutrient acquisition, and ion ratios of *C. camphora* seedlings under simulated saline regimes. This study is expected to advance our understanding of the mechanisms underlying salt-stress alleviation by AMF in *C. camphora* seedlings and help toward developing practical ways for soil restoration in coastal areas.

2. Materials and Methods

2.1. Plant Materials and AMF Preparation

C. camphora seeds were collected from 30 mother trees that were ~10 m away from each other at the campus of Zhejiang A & F University (ZAFU) (30°14′ N, 119°42′ E) in southeastern China [27]. In the last week of February 2017, the seeds were surface-sterilized with 5% NaClO for 10 min and were then rinsed with sterilized distilled water [28]. Subsequently, five seeds were sown in one plastic pot (16.5 × 18 × 12 cm) filled with 2 kg substrate. The substrate used in this experiment was a combination of field soil and peat at a ratio of 3:1 (v/v) that was exposed to gamma irradiation (25 KGy, 60 Co γ-rays) to eliminate indigenous microorganisms before use [29]. The local soil is acidic and belongs to the Hapludult soil type in Chinese Soil Taxonomy [30]. The soil properties are as follows: pH, 5.87; Olson P, 0.28 mg g^{-1}; total N, 0.75 mg g^{-1}; Na^+, 0.52 mg g^{-1}; K^+, 7.56 mg g^{-1}; Ca^{2+}, 7.23 mg g^{-1}; Mg^{2+}, 1.21 mg g^{-1}; Mn^{2+}, 0.38 mg g^{-1} [31]. Sixty days after germination, the seedlings (6 cm in height, and four leaves per plant) were thinned to one plant per

pot. During this experiment, the plants were grown in a naturally lit greenhouse, with a mean temperature and relative humidity of 30.1 °C and 68%, respectively. The pots were relocated weekly to reduce edge effects.

Two mycorrhizal fungal species, which are broad-spectrum and reportedly effective at improving plant resistance to salt stress [9,16], were selected as inocula: *Funneliformis mosseae* (BGC HUN03B) (isolated from the rhizosphere of *Roegneria kamoji* grown in Hunan Province, China) and *Rhizophagus irregularis* (BGC BJ09) (isolated from the rhizosphere of *Lycopersicon esculentum* grown in Langfang, Hebei Province, China) [32]. The two mycorrhizal inocula were obtained by multiplying separately for 5 months using *Sorghum bicolor* as the host plants in pots with sterilized fine sand as substrate [33]. The soil-based inocula, contained ~160 and 200 spores 10 g^{-1} of soil in *F. mosseae* and *R. irregularis*, respectively, along with chopped AM-colonized *S. bicolor* roots. The corresponding inocula were mixed thoroughly with the substrate before sowing the seeds in the pots. Before application, the fungal inocula were subjected to the highest possible number test [34].

2.2. Experimental Design and Treatments

The experiment was performed using 12 full factorial combinations of two factors: AMF regime and salt regime. Four AMF regimes (inoculation with sterilized AMF as the control, inoculation with *F. mosseae* or *R. irregularis*, either alone or in combination) and three salt regimes (0, 50, and 200 mM NaCl) were evaluated. In total, there were 12 treatment combinations, with six replicates per treatment. Mycorrhizal plants (AM plants) received 20 g of *F. mosseae*, *R. irregularis*, or the combined inoculum containing equal proportions of the two fungal species per pot. Non-mycorrhizal plants (NM plants) received the same amount of autoclaved inoculum, combining the two fungal species with an additional 20 mL of combined inoculum filtrate that was sieved through a 25 µm filter to provide similar microflora (excluding AMF) [35].

To prevent salt-induced shock to AMF development and plant fine root growth, NaCl treatment was started on 14 May 2017, 30 days after thinning and seedling establishment. Furthermore, to mimic the saline conditions occurring in most coastal areas of southern China, where salinity levels average between 0.1% (equivalent to 50 mM NaCl; low NaCl stress) and 0.4% (equivalent to 200 mM NaCl; high NaCl stress) [33], the three NaCl solutions (0, 50, and 200 mM) were gradually applied following the protocol of Qiu et al. [31] and conferred electrical conductivity (EC) of 0.22, 2.3, and 9.3 dS m^{-1}, respectively. Leaching was avoided by maintaining soil water below field capacity throughout the treatment. Soil EC was monitored and was adjusted once every 15 days with the corresponding NaCl solution. Plants were irrigated with distilled water when required. To ensure plants were alive, 10 mL of adjusted Hoagland solution was added to the pots weekly [33]. Seedlings were harvested 6 months after salinity stress, on 14 November 2017.

2.3. Measurements

At the end of the experiment, all the plants were gently separated from the substrate, rinsed with distilled water three times, and then separated into roots and shoots. Fresh roots were sub-sampled into two parts, one of which was used to determine mycorrhizal colonization in the roots. The percentage of roots colonized by AMF was determined by staining with 0.05% trypan blue in lactophenol [36]. Then, the samples were examined to determine the percentage of mycorrhiza using the gridline-intersection method [37].

The remaining shoots and roots were separately oven dried at 60 °C for 72 h, and their dry weights were recorded. Three dried samples that were randomly chosen from each treatment combination were ball-milled before elemental analysis.

Total N and P concentrations were measured using the Kjeldahl method and ammonium molybdate blue method, respectively [38]. The concentrations of K^+, Na^+, Ca^{2+}, Mg^{2+}, Cu^{2+}, Zn^{2+}, Fe^{2+}, and Mn^{2+} were measured using an AA−7000 atomic absorption spectrophotometer (Shimadzu, Kyoto, Japan) [39].

2.4. Data Analysis

Mycorrhizal dependence (*MD*) was calculated using the following equation [16]:

$$MD(\%) = \frac{DW_{AMF} - Avg(DW_{non-AMF})}{DW_{AMF}} \times 100$$

where DW_{AMF} is the biomass of AM plants, and $Avg(DW_{non-AMF})$ is the average biomass of NM plants under identical saline levels (n = 6).

To quantify salt-tolerance of the plants, selective transporting capacity (*STC*) of K^+ over Na^+ from roots to shoots was computed as follows [40]:

$$STC = \left(K^+/Na^+ \text{ in shoots}\right) / \left(K^+/Na^+ \text{ in roots}\right)$$

Data were analyzed using a two-way analysis of variance to evaluate the effects of salt, AMF, and their combination. Before analysis, all the data were subjected to the Shapiro–Wilk test for normality and Levene's test for equality of variance. Differences among treatments were determined using the least significant difference (LSD) at $p < 0.05$. Additionally, partial regression was explored to quantity the contribution of the other parameters of mycorrhizal plants to *MD*. All analyses were performed using SPSS v. 23.0 (SPSS Inc., Chicago, IL, USA) and R v. 4.0.3 [41]. Graphs were visualized using Origin 2018 software (Origin Lab Co., Northampton, MA, USA).

3. Results

3.1. Mycorrhizal Colonization and Plant Growth

NM plants showed no AMF colonization in the roots. Mycorrhizal colonization was determined microscopically in all AMF-inoculated plants, with values ranging from 15.9% to 77.9% (Figure 1). Root colonization of AM plants decreased significantly with increasing salinity. Importantly, the root colonization of plants inoculated with *F. mosseae* alone, *R. irregularis* alone, and the combined inoculum decreased by 55%, 60%, and 51%, respectively, under high salinity stress in comparison with the corresponding ones under non-saline conditions. A difference in root colonization was recorded among AMF treatments. For instance, mycorrhizal colonization was higher for *R. irregularis* alone compared to *F. mosseae* alone or the combined inoculum under non-saline and highest saline conditions. None of the significant interaction between AMF and salt regime on the mycorrhizal colonization of plant roots was observed (Table S1).

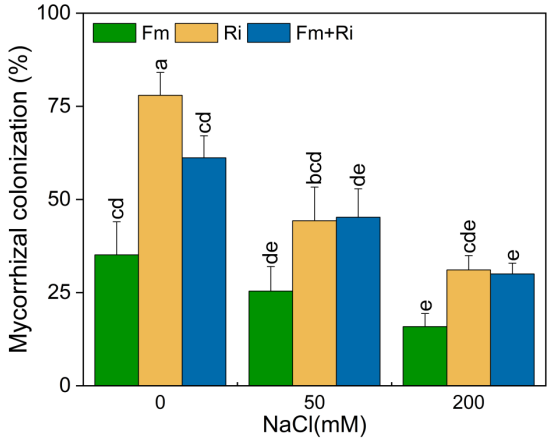

Figure 1. Mycorrhizal colonization in the root systems of *Cinnamomum camphora* plants under 0, 50 and 200 mM NaCl. Fm, Ri, and Fm+Ri represent the three mycorrhizal treatments: inoculation with sterilized mycorrhizal fungi, with *Funneliformis mosseae* or *Rhizophagus irregularis*, either alone or in combination, respectively. Values are presented as the mean ± SE (n = 3). Different lowercase letters indicate a significant difference according to LSD at $p < 0.05$.

The total dry weight of the plants varied with increasing salinity (Figure 2A). AMF enhanced the total dry weight of *C. camphora* under non-saline and low-salinity conditions. The highest total dry weight was consistently recorded for *R. irregularis*-inoculated plants. However, mycorrhizal association negatively affected the biomass accumulation of host plants under high-salinity conditions. Salinity and AMF alone caused various effects on the root:shoot ratio of plants (Figure 2B). Significant interactions between salt and AMF on the total dry weight and root:shoot ratio were observed (Table S1).

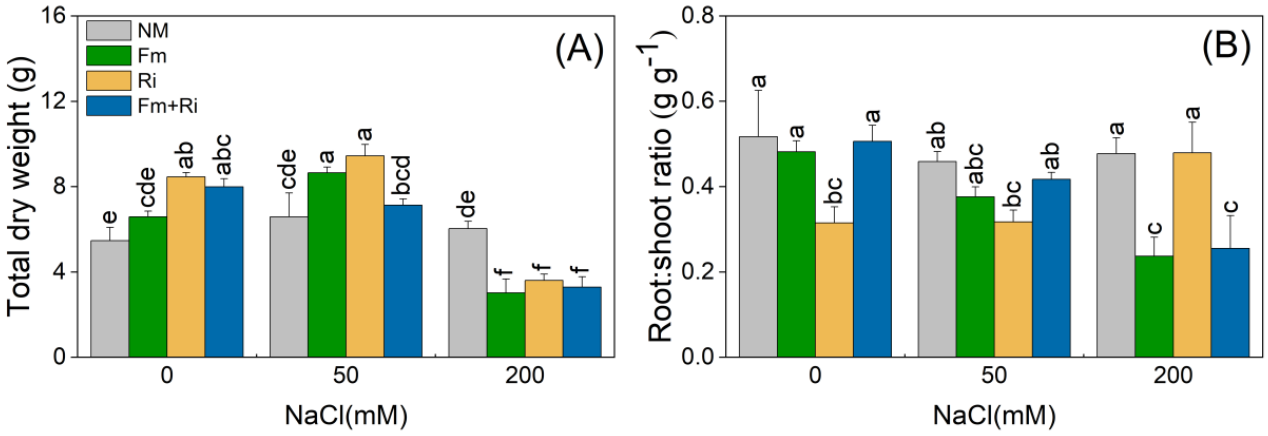

Figure 2. Effects of arbuscular mycorrhizal fungi on total dry weight (**A**) and root:shoot ratio (**B**) of *Cinnamomum camphora* plants under 0, 50, and 200 mM NaCl. NM, Fm, Ri, and Fm+Ri represent the four mycorrhizal treatments: inoculation with sterilized mycorrhizal fungi, with *Funneliformis mosseae* or *Rhizophagus irregularis*, either alone or in combination, respectively. Values are presented as the mean ± SE (n = 6). Different lowercase letters indicate a significant difference according to LSD at $p < 0.05$.

3.2. Nutrient Uptake and Allocation

AMF and salt stress had varied effects on macro- and micronutrient concentrations in shoots and roots, with mycorrhizal efficiency depending on the nutrients determined and AM fungal identification (Tables S2–S4). Total N concentrations in shoots of plants were not evidently affected by salinity, whereas the opposite result was observed for roots (Table S2). AM fungal species differently affected the N concentrations in shoots and roots, and their effects depended on saline levels (Tables S3 and S4). Salinity had variable effects on P concentrations in plants. Mycorrhizal colonization consistently caused P concentrations to increase in the shoots and roots under lower salinity conditions. The K^+ concentrations in shoots and roots of both NM and AM plants were inversely proportional to soil salinity. Mycorrhizal colonization, especially with *R. irregularis*, caused K^+ concentrations to increase significantly in roots at all salinity levels. The Na^+ concentrations in shoots and roots of both NM and AM plants showed a linear increase with increasing soil salinity. Na^+ concentrations in the shoots of NM plants, *F. mosseae*-inoculated plants, *R. irregularis*-inoculated plants, and combined inoculum-inoculated plants at the highest salinity were significantly higher than those of the corresponding plants under non-saline conditions (by 3694.4%, 468.0%, 913.1%, and 669.0%, respectively). Similarly, Na^+ concentrations in the roots of these four corresponding plants increased by 482.8%, 126.2%, 353.9%, and 271.4%, respectively. More Na^+ accumulated in roots compared to shoots. Mycorrhizal plants inoculated with single fungal species had significantly less Na^+ in their shoots compared to their NM counterparts at the highest salinity level. Ca^{2+}, Mg^{2+}, Zn^{2+}, Fe^{2+}, and Mn^{2+} concentrations in the shoots and roots differed between saline regimes and AM fungal species.

Furthermore, salinity caused Mg^{2+}:Na^+, K^+:Na^+, and Ca^{2+}:Na^+ shoot and root ratios to decline significantly in all plants (Figure 3). Under non-saline and low-salinity conditions, the shoot and root ratios of Mg^{2+}:Na^+, K^+:Na^+, and Ca^{2+}:Na^+ of mycorrhizal plants were

lower than those of NM plants (Figure 3A–C). Under higher salinity conditions, mycorrhizal fungi had various effects on the Mg^{2+}:Na^+, K^+:Na^+, and Ca^{2+}:Na^+ ratios of shoots and roots. Salinity caused the Na^+ shoot:root ratio to increase significantly (Figure 3D). Under non-saline conditions, the combined inoculum caused the Na^+ shoot:root ratio to increase significantly, whereas the other two AMF had no effects. Under lower salinity conditions, there was no difference in the Na^+ shoot:root ratio between NM plants and AM ones treated with any of the three AMF. Under higher salinity conditions, AMF caused the Na^+ shoot:root ratio to decrease significantly, except for the combined inoculum, and the lowest value was obtained for *R. irregularis*-inoculated plants.

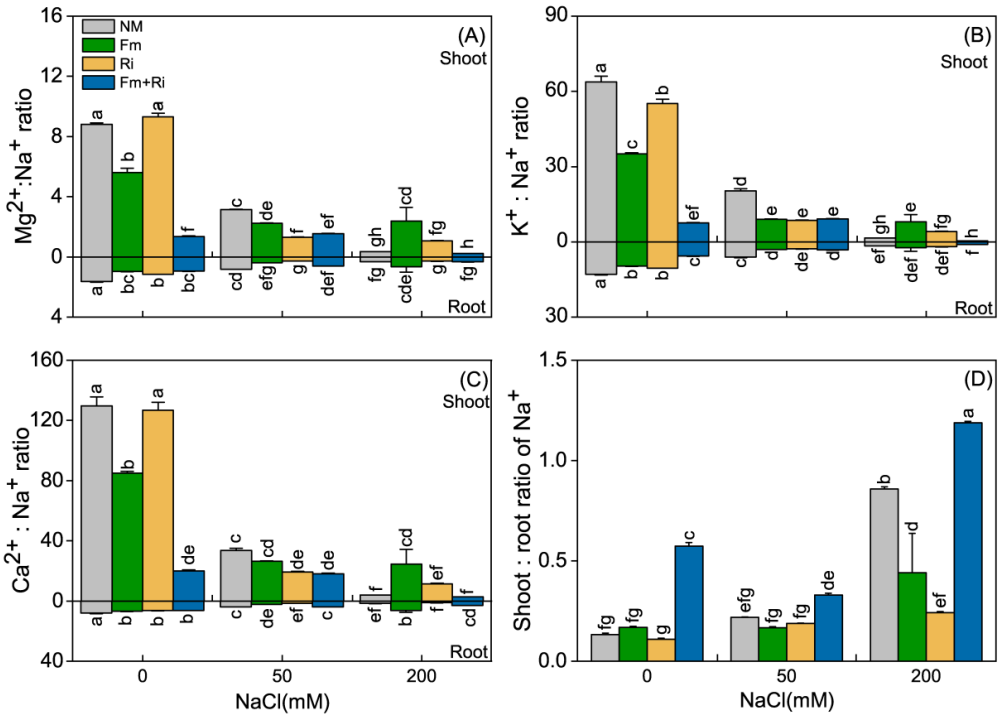

Figure 3. Effects of arbuscular mycorrhizal fungi on Mg^{2+}:Na^+ ratio (**A**), K^+:Na^+ ratio (**B**), Ca^{2+}:Na^+ ratio (**C**) in shoots and roots, and shoot:root ratio of Na^+ (**D**) of *Cinnamomum camphora* plants under 0, 50, and 200 mM NaCl. NM, Fm, Ri, and Fm+Ri represent the four mycorrhizal treatments: inoculation with sterilized mycorrhizal fungi, with *Funneliformis mosseae* or *Rhizophagus irregularis*, either alone or in combination, respectively. Values are presented as the mean ± SE (n = 3). Different lowercase letters indicate a significant difference for means of either root or shoot according to LSD at $p < 0.05$.

3.3. Mycorrhizal Dependence and Selective Transporting Capacity

The *STC* of plants decreased as salinity increased, however the opposite trend was observed for *F. mosseae*-inoculated plants (Figure 4A). The *STC* of mycorrhizal plants inoculated with single AM fungus was more than that of NM plants under the harshest salinity. In contrast, mycorrhizae provided no benefits under non-saline and lower salinity. The *MD* of AM plants decreased with increasing salinity (Figure 4B). Under non-saline and low salinity conditions, *MD* was positive, whereas under high salinity conditions, *MD* was negative. At all salinity levels, the highest values were detected for *R. irregularis*-inoculated plants.

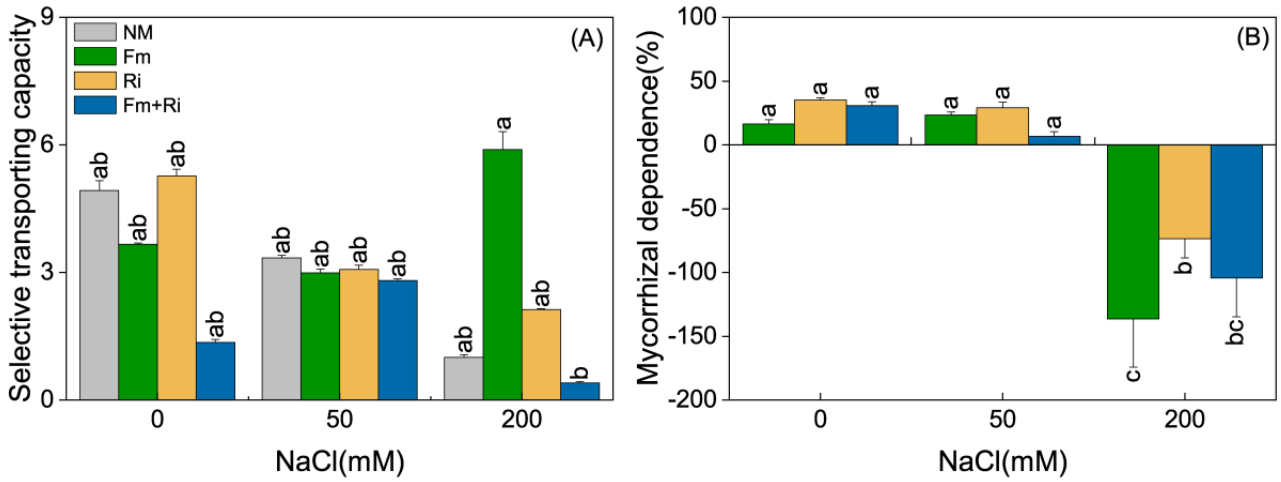

Figure 4. Effects of arbuscular mycorrhizal fungi on selective transporting capacity (*STC*) (**A**) and mycorrhizal dependence (*MD*) (**B**) of *Cinnamomum camphora* plants under 0, 50, and 200 mM NaCl. NM, Fm, Ri, and Fm+Ri represent the four mycorrhizal treatments: inoculation with sterilized mycorrhizal fungi, with *Funneliformis mosseae* or *Rhizophagus irregularis*, either alone or in combination, respectively. Values for *STC* are presented as the mean ± SE (n = 3), and those for *MD* are stated as the mean ± SE (n = 6). Different lowercase letters indicate a significant difference according to LSD at $p < 0.05$.

3.4. Mycorrhizal Dependence and Their Relationships with Other Plant Variables

MD was correlated with the root: shoot ratio, the ions concentrations, and the *STC* (Figure 5). Furthermore, to quantify their relationship strength, we constructed a fitted model (R^2 = 0.910, $p < 0.000$) as follows:

$$MD = 2.499\ X_1 + 1.327\ X_2 + 4.077\ X_3 + 2.066\ X_4 - 4.333\ X_5 + 4.143\ X_6 + 2.736\ X_7 - 1.367\ X_8 - 3.643\ X_9$$

where X_1~X_9 represent the *STC*, root: shoot ratio, shoot-P, shoot-Ca^{2+}, shoot-Mg^{2+}, shoot-Mn^{2+}, root-N, root-Na^+, and root-Mg^{2+}, respectively.

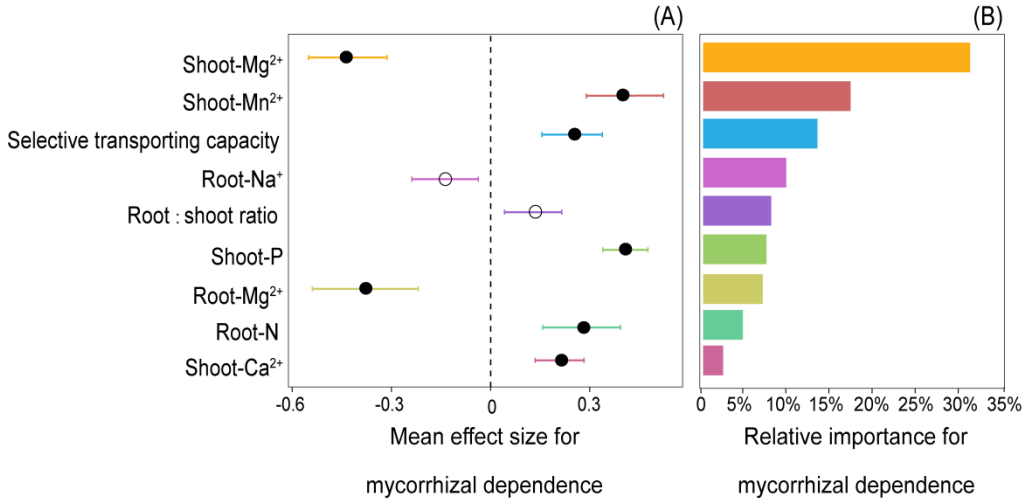

Figure 5. Mean effect sizes of observed variables on mycorrhizal dependence (*MD*) (**A**) and their relative contributions to variances of *MD* (**B**) in *Cinnamomum camphora* following partial regression. Abbreviations are as follows: shoot-Mg^{2+}, Mg^{2+} concentration in shoot; shoot-Mn^{2+}, Mn^{2+} concentration in shoot; *STC*, selective transporting capacity of K^+ over Na^+ from roots to shoots; root-Na^+, Na^+ concentration in root; shoot-P, P concentration in shoot; root-Mg^{2+}, Mg^{2+} concentration in root; root-N, N concentration in root; shoot-Ca^{2+}, Ca^{2+} concentration in shoot.

The shoot-Mn^{2+}, *STC*, root: shoot ratio, shoot-P, root-N, and shoot-Ca^{2+} were positively correlated with *MD*, whereas shoot-Mg^{2+}, root-Na^{+}, and root-Mg^{2+} were negatively correlated with *MD* (Figure 5A). Moreover, shoot-Mg^{2+}, shoot-Mn^{2+}, *STC*, root-Na^{+}, root: shoot ratio, and shoot-P together accounted for more than 86% of the variance in *MD*, which indicated their contribution to *MD* (Figure 5B).

4. Discussion

Our results showed that salinity caused certain parameters to decline significantly and others to increase significantly in the shoots and roots of *C. camphora*. The parameters that declined included total dry weight, mycorrhizal colonization, concentrations of K^{+}, Mg^{2+}:Na^{+}, K^{+}:Na^{+}, and Ca^{2+}:Na^{+} in shoots and roots. In comparison, the parameters that increased included Na^{+} concentrations in plant organs and the Na^{+} shoot:root ratio. However, AMF inoculation had generally beneficial effects on *C. camphora* parameters under low-salinity conditions. Our hypothesis that AMF, to some extent, would mediate salt-induced detrimental effects on *C. camphora* seedlings was supported. Moreover, mycorrhizal efficiencies varied with saline levels and AMF strains. Therefore, the second hypothesis was also proven. Importantly, our results showed that higher P and Mn^{2+} concentrations in shoot, root: shoot ratio, and *STC* appear to be responsible for the higher *MD* of *C. camphora* under saline conditions.

4.1. Improved Biomass with Mycorrhizal Inoculation

In this study, AM plants had higher biomass than NM ones under the control and lower salinity conditions (Figure 2), which means that AMF can somehow mediate the detrimental effects of salinity. This finding was consistent with reports on the trees of *Acacia auriculiformis* [42], *Olea europaea* [16], and *Citrus tangerine* [43]. Furthermore, the lowest fungal colonization and mycorrhizal dependence based on biomass occurred at the highest salinity level (Figures 1 and 4B), which may be induced by a high metabolic cost or an improved root respiration for the AM plants under severest salt stress [44]. This result supports the concept that severe salinity inhibits colonization through reduced plant growth and/or declining spore germination, hyphal growth, and branching [15,45]. This phenomenon occurs because a bidirectional relationship exists between host plants and their associated mycorrhizal fungi, whereby plants supply AMF with carbohydrates, while fungi improve the ability of the plants to access scarce and immobile nutrients [13,46]. Accordingly, certain factors that influence carbohydrate production and translocation to the roots [47], such as salinity, might cause root colonization and *MD* to decline.

4.2. Adjusting Na^{+} Uptake and Translocation with Mycorrhizal Inoculation

Analysis of Na^{+} uptake and its distribution between the shoots and roots showed that there was a continuous increase in Na^{+} concentrations and Na^{+} shoot:root ratios in NM plants with increasing salinity. However, in plants inoculated with single AM fungus, the responses of shoots were considerably lower, especially under the highest salinity (Figure 3 and Table S3). These findings were in line with those of previous reports [31,35,40,42], showing that AMF confer a regulatory effect on Na^{+} uptake and translocation from roots to shoots [35,39,48]. This phenomenon might be induced by the retention of Na^{+} in the root and intraradical fungal hyphae of AMF-inoculated plants, along with the inhibition of their translocation to shoots [3]. Alternatively, AMF might cause Na^{+} concentrations to decline through the dilution effect, due to growth enhancement [49,50]. Accordingly, the mediation of mycorrhizal colonization might partially enhance the salinity tolerance of AM plants. This is because elevated Na^{+} in soil or plant tissue could directly hamper the absorption of other nutrients through interfering with various transporters in the root plasma membrane, suppressing root growth by osmotic shock from Na^{+}, and reducing the population of soil bacteria [7,51]. However, other reports showed that AMF sometimes stimulate Na^{+} acquisition, particularly in halophytes, which generally accumulate more Na^{+} in shoots

compared to roots. This is possible because halophytes have certain anatomical properties, higher transpiration rates, and/or higher Na^+ transporter activity [3].

4.3. Enhanced Nutrient Concentratioin and Ionic Homeostasis with Mycorrhizal Inoculation

AMF enhance the nutrient acquisition of plants grown under salt-stressed conditions by promoting and/or selectively absorbing nutrients, as well as accelerating their transport from root systems [10,12]. The current study showed that AM plants had slightly or significantly higher P in both the shoots and roots, and higher K^+ in roots, compared to NM plants under lower salinity (Tables S3 and S4). Similar results were reported in previous studies [1,12,52]. The higher P concentration in AM plants could help maintain membrane integrity by reducing ionic leakage, limiting toxic ions within vacuoles, and enhancing selective ion uptake [35], and then ameliorates the detrimental effects of salinity [53]. Furthermore, the current study also showed that the values of tissue N:P ratios of NM plants were greater than 16 at all salinity levels (Figure S1), indicating that NM plants are exposed to P limitation [54]. Notably, the substrate soil in this study had a lower available P (0.28 mg g^{-1}) than the average concentration of soil P in China [55], suggesting that the experiment substrate was in P deficiency. Thus, the decreased tissue N:P ratios of plants inoculated with single AMF under low-salinity conditions (Figure S1) means that the magnitude of P limitation is reduced, which is mainly ascribed to the promotion of P uptake with mycorrhizal inoculation. Nevertheless, AMF significantly increased the N:P ratios of *C. camphora* plants in karst habitats, where the N:P ratios of the plants were even higher than 16 [52]. Similarly, *C. camphora* plants were exposed to P limitation in karst soil, whereas AMF greatly promoted N absorption but not P accumulation to compensate for P deficiency [52,56]. This discrepancy suggests that mycorrhizal plants grown in different habitats can adopt different strategies to deal with abiotic stress.

This study showed that mycorrhizal plants inoculated with single AM fungus had higher K^+:Na^+, Mg^{2+}:Na^+, and Ca^{2+}:Na^+ ratios than NM plants under the highest salinity conditions (Figure 3), indicating that mycorrhizal association favors ionic homeostasis in host plants [2]. These responses might reduce the detrimental effect of Na^+ and, consequently, enhance the salt tolerance of AM plants [9,43]. Some ion ratios, such as the K^+:Na^+ ratio in shoots, are accepted indicators for evaluating the plants' tolerance to salinity [49]. This is because compelling important functions, such as photosynthetic activity and nitrogen assimilation, require high K^+:Na^+ in shoots [7]. Improved K^+:Na^+ ratios recorded in the shoots of the current study were similar to those reported in *Acacia nilotica* [50], *Citrus tangerine* [43], *Trigonella foenum-graecum* [35], and *Valeriana officinalis* [2]. K^+ plays important roles in plant metabolism, including osmoregulation, stomatal regulation, and protein synthesis [16]. However, Na^+ and K^+ have identical physicochemical structures. Furthermore, the ability of Na^+ to compete with K^+ at binding sites is essential for various cellular functions [9]. A higher K^+:Na^+ ratio could hamper the disruption of K^+-mediated metabolic processes and influence the ionic balance of plants [12]. Moreover, the selective transporting capacity of K^+ over Na^+ from roots to shoots contributed greatly to *MD* on salt-stressed *C. camphora* plants (Figure 5). However, AMF-mediated ion homeostasis might be highly dependent on the salinity-tolerance of plant species, fungal isolates, and a specific combination of plant and AMF species [57]. Consequently, the selection of a suitable indicator, such as the K^+:Na^+ ratio, to quantify salt tolerance should be implemented with caution.

4.4. Underlying Mechanism for Mycorrhizal Dependence

Salinity-tolerance in plants is a complex ability that involves many changes at biochemical, physiological, and molecular levels [40]. Therefore, AMF-mediated alleviation of salt stress involves multiple mechanisms, including enhancement of nutrient uptake, maintenance of ionic homeostasis, and biochemical, morphological, physiological, molecular, and ultra-structural changes [9,10,12]. However, to date, a general principle to understand AM-conferred salt tolerance in plants is missing. For instance, Chandrasekaran et al. [9]

concluded that under saline conditions, mycorrhizal benefits are mainly related to enhance P nutrition in host plants. Feng et al. [22] suggested that the higher soluble sugar content in plant roots, rather than P status, is responsible for resistance to salt stress in mycorrhizal maize plants. This study showed that the underlying mechanism for enhancing performance in mycorrhizal plants could be related to P and Mn^{2+} concentrations in shoot, biomass allocation, and the selective transporting capacity of K^+ over Na^+ from roots to shoots (Figure 5). Similar to that suggested by Evelin et al. [11], these mechanisms might work in tandem to improve salt tolerance in mycorrhizal plants. The contradictory results across these studies might be due to differences in the characteristics of AMF or because there are specific compatible relationships between symbionts and environmental contexts [58]. Importantly, the identity of AMF and host plants is more important than other variables in predicting plant response to salinity [9]. The current study, based on a comprehensive consideration of salt-tolerance and mycorrhizal benefits, showed that *R. irregularis* was more efficient than *F. mosseae* and their combination for *C. camphora* seedlings. Therefore, selecting the most effective AMF for a specific plant species is critical to improve its effectiveness under stressful conditions.

5. Conclusions

Our results demonstrate that under low-salinity conditions, mycorrhizal colonization, especially with *R. irregularis* inoculation, confers benefits to the growth of *C. camphora* plants by enhancing the concentrations of P and Mn^{2+} in shoots, maintaining ionic homeostasis, adjusting biomass allocation, and consequently, increasing plant resistance to salt stress. Moreover, mycorrhizal efficiency differed with respect to fungal species and salinity levels. These results reinforce existing evidence that AMF can alleviate the growth inhibition induced by salinity, thus, enhancing plant performance. Furthermore, the mycorrhizal association between AMF and *C. camphora* is of great interest for vegetation restoration in coastal areas. Since the current study was conducted in controlled conditions, there should be caution in extrapolating the results in the field. Therefore, to advocate forestry-level applications, further studies involving a wider range of AMF species and exploring the variability and/or stability of AMF-conferred salt tolerance in the field is required.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13111882/s1. Supplementary Table S1. *F*-values and degree of freedom (in parenthesis) of two-way ANOVA for the effects of salt, arbuscular mycorrhizal fungi (AMF) and their interactive effects on the growth and physiochemical variables of *Cinnamomum camphora* plants. Significance levels: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant at $p > 0.05$. Supplementary Table S2. *F*-values and degree of freedom (in parenthesis) of two-way ANOVA for the effects of salt, arbuscular mycorrhizal fungi (AMF) and their interactive effects on the nutrient uptake and ion ratios of *Cinnamomum camphora* plants. Significance levels: **, $p < 0.01$; ***, $p < 0.001$; ns, not significant at $p > 0.05$. Supplementary Table S3. Influence of NaCl and arbuscular mycorrhizal fungi on the nutrient concentrations of shoots of *Cinnamomum camphora* plants. NM, Fm, Ri, and Fm+Ri represent the four mycorrhizal treatments: inoculation with sterilized mycorrhizal fungi, with *Funneliformis mosseae* or *Rhizophagus irregularis*, either alone or in combination, respectively. Values are presented as the mean ± SE ($n = 3$). Different lowercase letters indicate a significant difference according to LSD at $p < 0.05$. Supplementary Table S4. Influence of NaCl and arbuscular mycorrhizal fungi on the nutrient concentrations of roots of *Cinnamomum camphora* plants. NM, Fm, Ri, and Fm+Ri represent the four mycorrhizal treatments: inoculation with sterilized mycorrhizal fungi, with *Funneliformis mosseae* or *Rhizophagus irregularis*, either alone or in combination, respectively. Values are presented as the mean ± SE ($n = 3$). Different lowercase letters indicate a significant difference according to LSD at $p < 0.05$. Supplementary Figure S1. Effects of arbuscular mycorrhizal fungi on the ratios of nitrogen to phosphorus (N:P ratio) of *Cinnamomum camphora* plants under 0, 50, and 200 mM NaCl. NM, Fm, Ri, and Fm+Ri represent the four mycorrhizal treatments: inoculation with sterilized mycorrhizal fungi, with *Funneliformis mosseae* or *Rhizophagus irregularis*, either alone or in combination, respectively. Values are presented as the mean ± SE ($n = 3$). Different lowercase letters indicate a significant difference according to LSD at $p < 0.05$.

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Abbreviations

AMF	arbuscular mycorrhizal fungi
AM	arbuscular mycorrhizal
AM plants	mycorrhizal plants
NM plants	non-mycorrhizal plants
EC	Electrical conductivity
MD	mycorrhizal dependence
STC	selective transporting capacity of K^+ over Na^+ from roots to shoots
LSD	Least significant difference

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