

Effects of AMF on Root Growth and Nitrogen Uptake and Allocation in *Tamarix ramosissima* Seedlings and *Alhagi sparsifolia* under Drought Stress (Postprint)

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Abstract

Arbuscular mycorrhizal fungi (AMF) play crucial roles in plant drought resistance and nutrient acquisition; however, plant responses to AMF vary among different life forms under specific environmental stresses. This study examined the effects of AMF inoculation (non-inoculated control M- versus inoculated treatment M+) on root growth characteristics and nitrogen uptake and allocation in mixed plantings of *Tamarix ramosissima* (the dominant shrub in desert riparian forests of the lower Tarim River) and *Alhagi sparsifolia* (a common semi-shrub), compared with monoculture controls, under drought stress conditions (control: 70%±5±5% soil relative water content). The results demonstrated: (1) Under drought stress, mycorrhizal colonization rates decreased in both *Tamarix ramosissima* seedlings and *Alhagi sparsifolia*, whereas mixed planting significantly enhanced the mycorrhizal colonization rate of *T. ramosissima* seedlings ($P < 0.05$); (2) Under drought stress, the mixed planting M+ treatment significantly increased both aboveground and belowground biomass of *T. ramosissima* seedlings; (3) Under drought stress, AMF significantly increased fine root length and fine root surface area of both species across all planting patterns, significantly reduced the specific root length of *A. sparsifolia*, and the mixed planting M+ treatment significantly decreased the fine root specific root length of *T. ramosissima* seedlings; (4) Compared with monoculture, AMF significantly increased nitrogen uptake and the proportion allocated to aboveground parts in mixed-planted *T. ramosissima* seedlings under drought stress. Therefore, AMF exerts a significant compensatory effect on growth and nitrogen uptake of *T. ramosissima* seedlings coexisting with *A. sparsifolia* under drought stress, which may facilitate the successful establishment of *T. ramosissima* seedlings in the lower Tarim River region during their vulnerable growth period.

Full Text

Effects of Drought Stress and Arbuscular Mycorrhizal Fungi on Root Growth, Nitrogen Absorption, and Distribution in *Tamarix ramosissima* and *Alhagi sparsifolia* Seedlings

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Abstract

Arbuscular mycorrhizal fungi (AMF) play a crucial role in plant drought resistance and nutrient absorption, yet plant responses to AMF vary among different life forms under specific environmental stresses. This study examined the dominant shrub *Tamarix ramosissima* and the common subshrub *Alhagi sparsifolia* in the desert riparian forest of the lower Tarim River. We analyzed the effects of drought stress treatments (control group with $70\% \pm 5\%$ soil relative water content, experimental group with $20\% \pm 5\%$ soil relative water content), AMF inoculation (non-inoculated control vs. inoculated treatment), and planting patterns (monoculture vs. mixed planting of *T. ramosissima* and *A. sparsifolia*) on root growth and nitrogen absorption and allocation. The results demonstrated that: (1) Under drought stress, mycorrhizal infection rates in both *T. ramosissima* seedlings and *A. sparsifolia* decreased, yet mixed planting significantly increased the mycorrhizal infection rate in *T. ramosissima* seedlings ($P < 0.05$). (2) Under drought stress, mixed planting significantly increased both aboveground and belowground biomass in *T. ramosissima* seedlings. (3) Drought stress significantly increased fine root length and surface area in both species under mixed planting, while significantly decreasing the specific root length of *A. sparsifolia*. Additionally, mixed planting significantly reduced the fine root specific length of *T. ramosissima* seedlings. (4) Compared with monoculture, AMF significantly increased nitrogen uptake and aboveground nitrogen allocation ratio in *T. ramosissima* seedlings under drought stress. These findings indicate that AMF exerts a significant compensatory effect on the growth and nitrogen absorption of *T. ramosissima* seedlings when mixed with *A. sparsifolia* under drought stress, thereby facilitating the survival of *T. ramosissima* seedlings during their vulnerable growth period in the lower Tarim River region.

Keywords: arbuscular mycorrhizal fungi; drought stress; *Tamarix ramosissima*; *Alhagi sparsifolia*; nitrogen

Introduction

Plants coexisting in the same habitat engage in complex interspecific interactions, which in natural ecosystems typically manifest as competition for space

and resources that directly or indirectly inhibit each other's growth. In arid environments, plant growth is suppressed by drought stress, while soil microorganisms can enhance plants' capacity to absorb and utilize water and nutrients through symbiotic relationships. Arbuscular mycorrhizal fungi (AMF), among the most closely associated soil microbes with plants, form mutualistic symbioses with two-thirds of terrestrial plant species. These fungi develop hyphal networks that can reinfect other plant roots through infection points, creating common mycorrhizal networks (CMNs) that distribute water and nutrients among different individuals and promote plant growth under adverse conditions.

The lower reaches of the Tarim River constitute an extremely arid region harboring diverse plant life forms. Soil moisture and nitrogen consistently represent critical limiting factors for seed germination, seedling growth, and survival in this area. Previous research has demonstrated that AMF significantly expand plant root systems and facilitate water absorption under drought stress. Studies on common bean (*Phaseolus vulgaris*) have shown that AMF-plant root symbiosis enhances plant responses to drought, while long-term drought experiments on the perennial grass *Themeda triandra* revealed that inoculated plants exhibited substantially greater growth recovery than non-inoculated counterparts. AMF can also increase the activity of key nitrogen assimilation enzymes, thereby enhancing nitrogen absorption capacity. In nitrogen-limited regions, plants may compete for nitrogen resources, and AMF can directly or indirectly influence interspecific nitrogen uptake patterns.

The lower Tarim River region supports a degraded desert riparian forest where *Tamarix ramosissima* (Tamaricaceae) serves as a dominant constructive species with strong drought resistance and broad ecological adaptability. *Alhagi sparsifolia* (Leguminosae), a typical perennial subshrub in this region, plays an important role in sand fixation and commonly co-occurs with *T. ramosissima* populations, together maintaining the ecological stability of the desert area. Research has documented significant associations between AMF and desert riparian forest constructive species, with 84.62% of plants in natural and artificial communities in the lower Tarim River identified as mycorrhizal. Yang et al. isolated and identified *Glomus mosseae* as the dominant AMF species in the rhizosphere of *Populus euphratica* in this extreme arid region. Wang et al. similarly isolated multiple AMF species from the rhizosphere of *A. sparsifolia*, with *G. mosseae* as the dominant species. For *T. ramosissima* to fulfill its keystone role in promoting other herbaceous plants, it must survive the vulnerable seed-to-seedling transition stage while resisting drought stress and overcoming nutrient limitations, particularly nitrogen deficiency. Studies on inland rivers in arid regions have indicated that synchronization between flooding periods and *T. ramosissima* seed dispersal significantly promotes seedling establishment, highlighting the critical importance of water availability during this vulnerable growth phase.

While previous research has focused on AMF classification and interactions with single species, natural *T. ramosissima* communities are surrounded by numerous *A. sparsifolia* individuals, yet how these different species interact through

AMF networks to affect individual plant growth remains poorly understood. This study investigates the effects of AMF on root morphology and nitrogen absorption and allocation in *T. ramosissima* seedlings and *A. sparsifolia* under drought stress. We examine the ecological role of AMF during the vulnerable growth period of *T. ramosissima* seedlings, providing theoretical foundations for vegetation restoration and species diversity maintenance in the desert riparian forest of the lower Tarim River.

Materials and Methods

Experimental Apparatus

This study employed a Y-shaped pot system [Figure 1: see original paper]. Each 48 cm × 17 cm × 25 cm pot was divided into three compartments using nylon mesh barriers. The mesh was fixed to the pot walls with screws, where 20 μm nylon mesh permitted hyphal passage while blocking plant roots, and 0.45 mm mesh allowed only soil ions to pass while blocking both hyphae and roots. In this system, the donor compartment inoculated with AMF enabled hyphae to penetrate the 20 μm mesh into receptor compartments, infecting plant roots and forming a mycorrhizal network among different individuals within the microcosm apparatus. This design allowed investigation of hyphal network effects between the two plant species.

Experimental Materials and Treatments

The experimental plants, *T. ramosissima* and *A. sparsifolia*, were sourced from the lower Tarim River region. Uniform, plump seeds of both species were selected and sown in pots for outdoor germination at the greenhouse cultivation base of Xinjiang Normal University. The experimental substrate consisted of sieved sandy soil that underwent continuous moist heat sterilization at 0.14 MPa and 121°C for 2 hours. The AMF inoculum comprised a 1:1 mixture of *Glomus etunicatum* and *G. mosseae* obtained from the Institute of Microbial Application, Xinjiang Academy of Agricultural Sciences, with a spore density of 400 per 10 kg soil. Healthy, uniformly growing seedlings approximately 10 cm tall were retained after thinning, with three seedlings per compartment.

The experiment employed a three-factor, two-level factorial design: soil moisture (70% ± 5% relative water content as control, 20% ± 5% as drought stress), inoculation treatment (non-inoculated vs. inoculated), and planting pattern (monoculture vs. mixed planting). This yielded eight treatment combinations (Table 1). Soil moisture was monitored using a WET-2 portable moisture meter and maintained through gravimetric water supplementation. After 120 days of drought stress treatment, during which normal seedling growth was ensured, 10 mL of 15N-labeled ammonium nitrate was uniformly injected at ten symmetrically distributed points in the soil for tracer analysis. Plants were harvested after 15 days for index determination.

Index Determination and Methods

Plant height, basal diameter, and crown width were measured directly using rulers. Aboveground and belowground biomass were harvested separately and dried at 80°C to constant weight. Dried samples were ground, and at least 0.5 g was sealed in centrifuge tubes for total nitrogen content and nitrogen allocation ratio determination at the Isotope Analysis and Testing Center of the Institute of Botany, Chinese Academy of Sciences. Root morphology parameters were analyzed by scanning graded root systems using an Epson V700 scanner and Japan Rhizo software. Mycorrhizal infection status was assessed using trypan blue staining and microscopic observation.

The following formulas were used for basic data analysis:

- $Ndff = (15N \text{ abundance in sample} - \text{natural abundance}) / (15N \text{ abundance in fertilizer} - \text{natural abundance}) \times 100$
- This represents the contribution rate of ^{15}N -labeled fertilizer to plant total nitrogen content (natural abundance of ^{15}N -labeled ammonium nitrate used: 0.365%)
- Nitrogen uptake from $^{15}N = \text{Dry mass} \times \text{Total nitrogen percentage} \times Ndff$
- Nitrogen allocation ratio = Nitrogen uptake in aboveground or belowground parts / Total nitrogen uptake $\times 100$

Data Analysis

All experimental data were processed using Excel for mean and standard error calculations and graphing. SPSS 19.0 was used for multi-factor ANOVA and multiple comparison analysis to determine significant differences among treatment indicators ($\alpha = 0.05$).

Results

Effects of AMF on Mycorrhizal Infection Rates Under Drought Stress

AMF effects on mycorrhizal infection rates differed between the two species under varying water treatments (Table 2). In control groups, a few arbuscules and vesicles were observed in *A. sparsifolia* roots, possibly associated with legume rhizobium symbiosis. No mycorrhizal infection, hyphal fragments, or arbuscule/vesicle structures were detected in *T. ramosissima* under non-inoculated conditions. Under drought stress, mycorrhizal infection rates decreased significantly in both species under monoculture ($P < 0.05$), with a more pronounced reduction in *T. ramosissima*. Although drought stress also reduced infection rates under mixed planting, *T. ramosissima* exhibited significantly higher infection rates than *A. sparsifolia*.

Effects of AMF on Plant Biomass and Root-Shoot Ratio Under Drought Stress

Drought stress significantly reduced aboveground and belowground dry weight in both species (Table 3). However, AMF inoculation promoted growth in both plants. Under monoculture, inoculation significantly increased *A. sparsifolia* biomass ($P < 0.05$). Under mixed planting, inoculation enhanced biomass in both species and particularly increased *T. ramosissima* aboveground and belowground biomass by 47.5% and 21.0%, respectively.

AMF also affected root-shoot ratios (Figure 2). Under drought stress, inoculation significantly increased the root-shoot ratio of *T. ramosissima* seedlings under mixed planting. The root-shoot ratio of *T. ramosissima* seedlings showed an increasing trend under inoculation, while that of *A. sparsifolia* increased initially then decreased. Under monoculture, inoculation significantly increased the root-shoot ratio of *A. sparsifolia* but not *T. ramosissima*. Under mixed planting, inoculation significantly increased root-shoot ratios in both species.

Effects of AMF on Root Morphology Under Drought Stress

AMF effects on root morphology were most direct (Tables 4-6). Drought stress decreased root length and surface area in both species, while AMF increased these parameters and reduced specific root length. Under drought stress, monoculture inoculation significantly increased fine root length (<2 mm) in both species ($P < 0.05$) but not coarse root length (>2 mm). Inoculation significantly increased fine root surface area in *A. sparsifolia* but not in *T. ramosissima*. Mixed planting with inoculation significantly increased coarse root length and fine root surface area in *T. ramosissima* seedlings.

Under drought stress, both monoculture and mixed planting with inoculation significantly reduced coarse root specific length in *A. sparsifolia*, while mixed planting significantly reduced fine root specific length in *T. ramosissima* seedlings. This suggests that mycorrhizal hyphae may substitute for some root absorption functions.

Effects of AMF on Nitrogen Uptake and Distribution Under Drought Stress

AMF affected total nitrogen uptake differently in the two species under drought stress (Figure 3). Inoculation increased total nitrogen content in *T. ramosissima* seedlings but decreased it in *A. sparsifolia*. Mixed planting under drought stress significantly increased total nitrogen in *T. ramosissima* ($P < 0.05$), indicating that mixed planting with AMF promotes nitrogen uptake in *T. ramosissima* seedlings and regulates nutrient deficiency.

AMF also influenced above- and belowground nitrogen allocation ratios (Figure 4). Under drought stress, *T. ramosissima* seedlings showed reduced nitrogen allocation to both above- and belowground parts, but mixed planting with in-

oculation significantly increased aboveground nitrogen allocation ($P < 0.05$), enabling *T. ramosissima* seedlings in mixed culture to absorb more nitrogen.

Discussion

Mycorrhizal infection rate represents the fundamental condition for plant root-AMF interactions, and different symbiotic relationships with various hosts affect host growth characteristics differently. Wang et al. isolated multiple AMF species from the rhizosphere of *A. sparsifolia*, with *G. mosseae* as the dominant species. Our experimental inoculum comprised a mixture of *G. etunicatum* and *G. mosseae*, which may explain the higher infection rate in *A. sparsifolia* compared to *T. ramosissima*. However, under drought stress with mixed planting, *T. ramosissima* exhibited significantly higher infection rates than *A. sparsifolia*, suggesting that under mixed growth conditions, AMF may preferentially promote *T. ramosissima* seedling growth by transferring more water and nutrients to this species, thereby helping it survive the vulnerable seedling stage.

Our findings show that inoculated plants had higher total biomass than non-inoculated plants, consistent with Merrild et al.'s conclusion that mycorrhizal networks can increase average plant size. However, Weremijewicz et al. found that mycorrhizal networks promote growth of larger plants while inhibiting smaller ones. In our study, AMF effects on above- and belowground biomass differed between species and water treatments. Under drought stress, mixed planting with inoculation significantly increased *T. ramosissima* seedling biomass, while monoculture inoculation significantly increased *A. sparsifolia* biomass. This indicates that AMF may enhance water retention capacity in *A. sparsifolia* under drought, but in mixed culture, AMF more strongly promotes *T. ramosissima* root development.

Under drought stress, mixed planting significantly promoted coarse root length and fine root surface area in *T. ramosissima* seedlings, suggesting that AMF favor root development in this species. This enables deeper soil penetration by coarse roots and expanded absorption area by fine roots, enhancing water and nutrient acquisition. Han et al. demonstrated that roots with diameters < 2 mm perform the primary absorption function, and Veiga et al. showed that AMF colonization induces finer root systems that facilitate water and nutrient uptake. Our results indicate that AMF hyphae may substitute for some root absorption functions, as evidenced by reduced specific root length in colonized plants. The differential growth rates between *T. ramosissima* (a constructive shrub species) and *A. sparsifolia* (a subshrub) create competition, and AMF appear to preferentially promote *T. ramosissima* seedling root development while having less pronounced effects on *A. sparsifolia*, thereby balancing the competitive relationship under drought stress.

Using ^{15}N isotopic tracing provides convenient comparison of nitrogen allocation patterns between species. Liu et al. detected ^{15}N in tobacco roots, stems, and leaves after AMF inoculation, and we similarly detected ^{15}N in both study

species, with differential distribution between above- and belowground parts. Ma et al. found reduced rhizosphere soil nitrogen in drought-stressed *Bombax ceiba* inoculated with AMF, confirming that nitrogen can be supplied to plants via hyphal networks. Our results show that under normal water conditions (70% soil relative water content), AMF effects on both species were not significant, likely because adequate soil moisture facilitates nitrogen mobility, reducing plant dependence on mycorrhizae. However, under drought stress, *T. ramosissima* seedlings stored most AMF-acquired nitrogen in aboveground tissues, creating a nitrogen “sink” that accelerates seedling growth and helps them rapidly pass through the vulnerable establishment phase.

Conclusions

1. Drought stress reduces AMF colonization in seedlings of both desert plant species in the lower Tarim River, while mixed planting enables drought-stressed *T. ramosissima* seedlings to maintain higher mycorrhizal infection rates than *A. sparsifolia*.
2. Under drought stress, AMF inoculation significantly increases biomass and promotes growth of both desert plant seedlings. Specifically, when mixed with *A. sparsifolia*, AMF markedly enhances *T. ramosissima* seedling root development by significantly increasing coarse root length and fine root surface area, substantially improving water and nutrient acquisition capacity.
3. Under drought stress, AMF differentially affects total nitrogen uptake between monocultured species, increasing total nitrogen in *T. ramosissima* while decreasing it in *A. sparsifolia*. Mixed planting with AMF significantly enhances nutrient absorption, particularly aboveground nitrogen content, in *T. ramosissima* seedlings.

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