



Nutrient Uptake and Distribution in Mycorrhizal Cuttings of *Populus × canadensis* ‘Neva’ Under Drought Stress

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Abstract

Arbuscular mycorrhizal fungi (AMF) have been reported to improve the resistance to drought stress in some plant species. The aim of this study was to evaluate the effects of *Rhizophagus irregularis* inoculation on the growth, photosynthetic capacity, nutrient uptake, and nutrient distribution of poplar cuttings under drought stress. The experiment was performed with a randomized block design with two factors: (i) AMF treatment, inoculated with *R. irregularis* (AM) or not (NM); (ii) drought treatment, well-watered (WW, 70–75% of field capacity), mild stressed (MS, 50–55% of field capacity), or severe stressed (SS, 30–35% of field capacity). The results showed that *R. irregularis* colonized more than 70% of the roots of poplar cuttings. Drought stress limited the plant growth and photosynthetic capacity of poplar, while inoculation increased the plant height, stem diameter, stem dry weight, root dry weight, net photosynthetic rate (P_N), stomatal conductance (g_s), and intrinsic water use efficiency (WUE_i) regardless of the drought stress treatment. Drought stress decreased the absorption of nutrients and affected their distribution in plant tissues. Regardless of drought stress treatment, inoculation increased the concentrations of Ca and Mn in leaves and the concentration of Cu in roots. Under mild drought stress conditions, the contents of P, Ca, Cu, Fe, and Zn increased significantly in the leaves of inoculated plants, while the contents of P, Ca, Fe, and Mn increased significantly in the roots. Under severe drought stress, inoculation decreased the distribution of N, P, K, and Mg in the leaves; the distribution of K, Ca, Mn, and Zn in roots; and the distribution of Cu in roots. Moreover, a principal components analysis showed that under well-watered and severe drought stress conditions, the inoculation of poplars with *R. irregularis* could significantly increase the absorption of nutrients. The results of a correlation analysis indicated that the growth parameters and gas exchange parameters positively correlated with the concentrations of leaf P, K, Ca, Fe, Mn, Cu, and Zn. Photosynthetic capacity, nutrient absorption, and a change in nutrient distribution were enhanced in the mycorrhizal poplar cuttings, which resulted in enhanced growth and a limited loss of biomass during drought stress compared with the non-mycorrhizal cuttings.

Keywords AM · Nutrient uptake · Nutrient distribution · Poplars

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1 Introduction

Populus species and their hybrids have high economic value and are cultivated worldwide (Feodorova and Alexandrov 2020). *Populus × canadensis* ‘Neva’, a hybrid of *P. nigra* × *P. deltoides*, is widely planted in China as a woody species under intensive management (Li et al. 2021). The fast-growing poplar species/genotypes are generally vulnerable to drought stress owing to their high requirement for water (Yi et al. 2020).

Drought is considered a severe abiotic stress that causes plant growth inhibition. In general, drought stress can reduce the availability of nutrients in the soil, the absorption of nutrients by roots, the transport from roots to aboveground

parts, and the distribution among plants (Hussain et al. 2019). Under drought stress, phosphorus (P) and potassium (K) contents usually decrease (Püschel et al. 2021; Qi et al. 2019). The nutritional disturbance occurs in poplars when they are under water deficit (Tripathi et al. 2018).

The fossil records suggest that arbuscular mycorrhiza (AM), which appeared 400 million years ago (Walker et al. 2018), are the most common and widely distributed type of plant symbiosis (Brundrett and Tedersoo 2018). AM are important mutualistic symbioses formed between fungi from the phylum *Glomeromycota* and more than 72% of terrestrial plants (Brundrett and Tedersoo 2018). The spread of arbuscular mycorrhizal fungal (AMF) mycelia can increase the absorption area of the host plant's root in the soil. Moreover, AMF rely on photosynthates from the host to complete their life span and supply water and mineral nutrients to the host (Ortuño et al. 2018; Wu et al. 2017a). AMF can enhance plant drought resistance by improving plant nutrition. On the one hand, AMF can alleviate the decrease in soil available nutrients caused by drought by improving the absorption of slowly diffusing mineral ions, such as PO_4^{2-} and Zn^{2+} (Hu et al. 2017; Watts-Williams et al. 2019). A previous study identified a positive effect of the AMF *Rhizophagus irregularis* and *R. arabicus* on drought resistance of *Sorghum bicolor* by increasing nutrient uptake (Symanczik et al. 2018). Alternatively, AMF regulates the ion and osmotic balances in plants under drought stress (Liu et al. 2020). Potassium accumulation in tobacco seedlings was regulated by AMF, and mycorrhizal tobacco seedlings had a better osmotic balance than the uninoculated control under drought stress (Liu et al. 2020). Alterations in the uptake, distribution, and composition of nutrients were observed in apple, palm, and *Ailanthus altissima*, inoculated with AMF under different soil conditions (Costa et al. 2021; Nejad et al. 2021; Zai et al. 2021). Exogenous inoculation with *R. irregularis* can increase the distribution of calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), and zinc (Zn) to the leaves of poplar (Wu et al. 2018). Arbuscular mycorrhizal fungus modulated Cd/Zn accumulation and distribution in poplar (De Oliveira et al. 2019). Alterations in the concentrations and distribution of nutrients may lead to changes in the photosynthetic capacity (Wu et al. 2018; Zai et al. 2021).

Previous research had confirmed that the shoot biomass and transpiration rates of poplars could be increased by *Rhizophagus irregularis* under cadmium (Cd) stress. (De Oliveira et al. 2019). Inoculation with AMF increased the area of absorption of the poplar roots and enhanced the absorption capacity of the roots for nitrate (NO_3^-) (Wu et al. 2020). An improvement in photosynthetic capacity and drought tolerance of *P. × canadensis* 'Neva' by AMF was found in a previous study (Liu et al. 2015), but the influence of AMF on nutrient uptake and distribution of *P. × canadensis* 'Neva' remains elusive. This study was conducted to determine the

effects of AMF on the nutrient contents and their distribution in different organs of *P. × canadensis* 'Neva' under different drought stress levels.

2 Material and Methods

2.1 Plant Material and AM Colonization

The cuttings (15 cm in length) of *P. × canadensis* 'Neva' used in this study were obtained from a nursery of poplar cuttings that were produced vegetatively in Rougu county, Yangling district, Shaanxi Province, China. The surface disinfection process of cuttings consisted of soaking them in 75% (v/v) ethanol for 15 s and then rinsing them three times with sterile distilled water for 10 s at a time. The surface-disinfected cuttings were planted with 2 cm exposed outside of the pots (19.5 × 21.5 cm), which contained 5 kg of soil substrate.

The substrate was a mixture of soil and sand (1:1, v/v) that was autoclaved at 121 °C for 2 h under pressure (0.11 MPa), and then placed in a storage room for 3 days before use. Soil (0–20 cm) was obtained from a nursery on the campus of Northwest A&F University (Yangling, China) and sieved with a 2-mm mesh. The soil contained 16.21 g kg⁻¹ soil organic matter, 12.78 mg kg⁻¹ available P, 33.89 mg kg⁻¹ available nitrogen (N), and 132.54 mg kg⁻¹ available K. The soil pH was 7.6 (soil: water, 1:5). Thoroughly washed river sand was mixed with soil.

The inoculum of *Rhizophagus irregularis* (Blaszk, Wubet, Renker & Buscot) Walker & Schüßler (BGC B109) was supplied by the Institute of Plant Nutrition and Resources, Beijing Academy of Agriculture and Forestry Sciences (Beijing, China). The AMF inoculum consisted of soil, infected root fragments, spores, and hyphae. The inoculum (20 g) was placed next to the cutting in the pot, while the non-inoculated treatments were provided with 20 g of autoclaved inoculum, to ensure consistent with the nutritional environment of the inoculation treatment.

2.2 Experimental Design and Growth Conditions

The experiment was performed using a randomized block design with two factors: (i) AM treatment, inoculated with *R. irregularis* (AM) or not (NM); (ii) drought treatment, well-watered (WW, 70–75% of field capacity), mildly stressed (MS, 50–55% of field capacity), or severely stressed (SS, 30–35% of field capacity). Field capacity was calculated as follows: $X = (\text{saturated soil weight} - \text{dry soil weight}) / \text{dry soil weight} \times 100\%$.

The pots were weighed every day to control the soil water content. The experiment included six treatments. One cutting was planted per pot, and three pots were merged into

one replicate. Each treatment contained four replicates, and there were 72 cuttings in this experiment.

The experiment was carried out in a greenhouse at Northwest A&F University, Shaanxi Province, China, with 12–14 h light per day, a relative humidity of 55–78%, and a temperature of 25–35 °C.

During the experiment, cuttings were fertilized with 100 mL Hoagland's solution every 2 weeks and grown under well-watered conditions. Thirty days after planting, the drought treatment started and continued for 60 days. The positions of pots were changed every other week.

2.3 Plant Growth Parameters and Mycorrhizal Colonization

Cuttings were harvested 90 days after planting. The plant height was determined by a tape (Swordfish, China) and the stem diameter with Vernier calipers (ECV150C, China). The roots from each treatment were collected, washed with tap water to remove the soil particles, and dried with paper towels. The fresh weights of leaves, stems, and roots were recorded. The dry weight of leaves, stems, and roots was recorded after oven drying to a constant weight at 80 °C. Parts of the roots were cut into 1-cm-long fragments and stained with trypan blue (Phillips and Hayman 1970). A total of 200 root segments were collected for each treatment. The rates of AM colonization were examined using the gridline intercept method (Giovannetti and Mosse 1980).

2.4 Gas Exchange Parameters

The leaf without visible injury was selected for the gas exchange measurements between 08:00 and 13:30 before harvest. The net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO₂ concentration (C_i), and transpiration rate (E) were measured with a Li-Cor 6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA) and red/blue LED. All of the measurements were conducted with the following parameters: photosynthetically active irradiation of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, a CO₂ concentration of 400 $\text{cm}^3 \text{m}^{-3}$, and a leaf temperature of 50 °C. The intrinsic water use efficiency (WUE_i) was calculated as follows: $WUE_i = P_N/g_s$.

2.5 Nutrient Analysis

The nutrient analysis was performed using ground and homogenized dry samples of roots, stems, and leaves. The N concentration was determined as described by Kong et al. (2015) using 0.2 g of dried leaves, stems, and roots, and the P concentration was determined using 1 g of dried leaves, stems, and roots that were digested with HNO₃-HClO₄ using the vanadomolybdate method (Wu et al. 2018). The

K, Mg, Ca, Fe, Zn, copper (Cu), and Mn concentrations were determined as described by Nisha and Rao (2017) using an atomic absorption spectrophotometer (Hitachi Z-2000, Tokyo, Japan). The nutrient contents equal the nutrient concentrations multiplied by the dry weight. The distribution of elements in the leaf, stem, and root equal nutrient contents divided by the total element contents.

2.6 Statistical Analysis

The data were examined for normality and homogeneity. The differences in associated measured parameters according to AM status, water status, and their interaction were analyzed using SPSS v. 17.0 for Windows (SPSS, Inc., Chicago, IL, USA). A two-way analysis of variance (ANOVA) was used to test the effects of drought, inoculation, and their interactions at $P \leq 0.05$. Multiple comparisons were performed using a Duncan's post-hoc test. The principal component analysis (PCA) of the nutrient parameters was analyzed using MetaboAnalyst 4.0 (Chong et al. 2018). Correlations between gas exchange parameters and leaf nutrient concentrations were analyzed by Pearson's correlation coefficients.

3 Results

3.1 Plant Growth and AM Colonization

The AM colonization is significantly influenced by drought treatment, AM treatment, and their interaction (Table 1). The colonization rate of *R. irregularis* is higher than 70% in

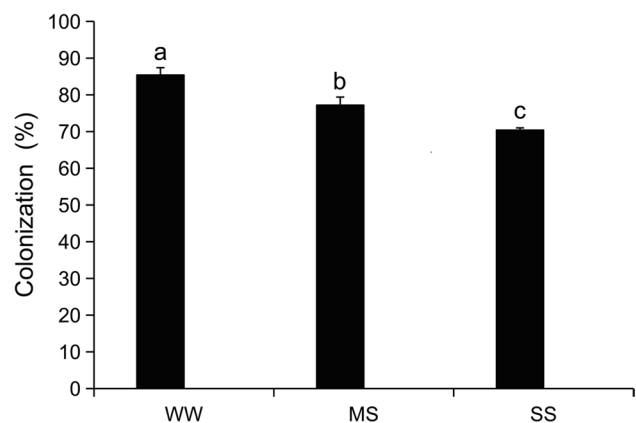


Fig. 1 Frequency of mycorrhizal colonization. WW, well-watered; MS, mildly stressed; SS, severely stressed. Values with different letters indicate significant differences (Duncan's test $P=0.05$, $n=4$)

Table 1 Results of a two-way ANOVA for the effects of drought, *Rhizophagus irregularis* inoculation, and their interaction on various parameters of *Populus × canadensis* ‘Neva’

Index	Drought		AMF		Drought × AMF	
	F	P	F	P	F	P
Colonization	633.98	0.00**	55.22	0.00**	55.22	0.00**
Plant height	586.98	0.00**	192.53	0.00**	9.22	0.00**
Stem diameter	203.01	0.00**	53.00	0.00**	1.39	0.29 ns
Dry weight of leaves	37.85	0.00**	8.31	0.01*	2.24	0.15 ns
Dry weight of stems	233.67	0.00**	1151.48	0.00**	156.57	0.00**
Dry weight of roots	99.27	0.00**	48.51	0.00**	0.19	0.83 ns
Leaf N concentration	45.52	0.00**	0.41	0.53 ns	4.75	0.03*
Stem N concentration	35.36	0.00**	11.06	0.00**	2.51	0.12 ns
Root N concentration	4.35	0.04*	0.24	0.64 ns	2.08	0.17 ns
Leaf P concentration	8.51	0.00**	73.19	0.00**	4.95	0.03*
Stem P concentration	58.87	0.00**	66.91	0.00**	9.30	0.00**
Root P concentration	5.09	0.03*	202.96	0.00**	12.00	0.00**
Leaf K concentration	56.42	0.00**	17.72	0.00**	0.27	0.77 ns
Stem K concentration	0.18	0.84 ns	0.48	0.50 ns	4.90	0.03*
Root K concentration	31.28	0.00**	1.62	0.23 ns	33.72	0.00**
Leaf Ca concentration	124.28	0.00**	14.46	0.00**	11.88	0.00**
Stem Ca concentration	2.69	0.11 ns	59.56	0.00**	3.95	0.04*
Root Ca concentration	4.25	0.04*	7.96	0.02*	6.83	0.01*
Leaf Mg concentration	12.31	0.00**	0.80	0.39 ns	9.24	0.00**
Stem Mg concentration	1.01	0.39 ns	1.07	0.32 ns	4.04	0.05 ns
Root Mg concentration	268.86	0.00**	90.24	0.00**	15.56	0.00**
Leaf Fe concentration	10.11	0.00**	11.31	0.00**	0.72	0.51 ns
Stem Fe concentration	7.21	0.01*	33.92	0.00**	13.42	0.00**
Root Fe concentration	17.06	0.00**	5.73	0.03*	1.82	0.21 ns
Leaf Mn concentration	78.31	0.00**	1232.65	0.00**	35.35	0.00**
Stem Mn concentration	0.65	0.54 ns	35.86	0.00**	1.30	0.31 ns
Root Mn concentration	110.16	0.00**	26.00	0.00**	53.80	0.00**
Leaf Cu concentration	95.51	0.00**	4.32	0.06 ns	0.90	0.43 ns
Stem Cu concentration	8.84	0.00**	78.59	0.00**	0.52	0.61 ns
Root Cu concentration	103.97	0.00**	80.08	0.00**	4.52	0.03*
Leaf Zn concentration	534.62	0.00**	36.22	0.00**	18.02	0.00**
Stem Zn concentration	56.48	0.00**	79.02	0.00**	6.75	0.01*
Root Zn concentration	10.92	0.00**	270.51	0.00**	28.18	0.00**

AMF, AM treatment; * $P \leq 0.05$, ** $P \leq 0.01$, ns, non-significant

all the inoculated treatments; no mycorrhizal colonization is observed in non-inoculated plant roots (Fig. 1).

Plant height and stem diameter are significantly influenced by drought treatment and AM treatments (Table 1). Compared with non-inoculated treatments, the inoculation increases plant height and stem diameter under the different water regimes, while drought stress decreases the plant height and stem diameter for both non-inoculated and inoculated treatments (Fig. 2).

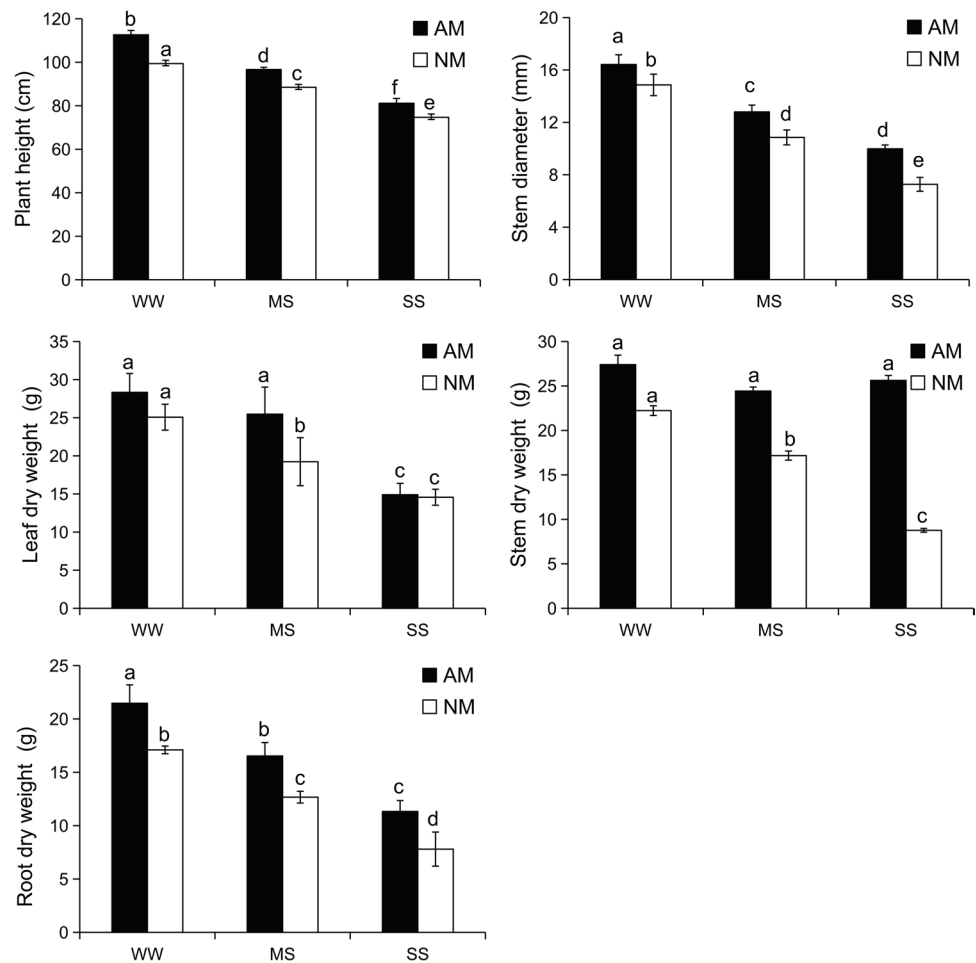
Drought treatment and AM treatments had significant effects on the dry weights of leaves, stems, and roots (Table 1). Compared with non-inoculated treatments, inoculation increases the stem and root dry weights under the different

water regimes, while drought stress decreases the root dry weight for both inoculated and non-inoculated treatments (Fig. 2).

3.2 Gas Exchange Parameters

Drought treatment and AM treatments had significant effects on the leaf gas exchange parameters (Fig. 3). Drought stress decreases P_{N_s} , g_{s_s} , C_i , E , and WUE_i , while inoculation increases C_i and E under well-watered and severe drought stress and increases P_{N_s} , g_{s_s} , and WUE_i regardless of drought stress treatment (Fig. 3).

Fig. 2 Effect of AM fungus and drought condition on plant growth parameters. WW, well-watered; MS, mildly stressed; SS, severely stressed; AM, inoculated with *Rhizophagus irregularis*; NM, non-mycorrhizal. Values with different letters indicate significant differences (Duncan's test $P=0.05$, $n=4$)



3.3 Macronutrient Concentrations

The concentration of P in all plant tissues, Ca in leaves and roots, and Mg in roots is significantly affected by drought stress, inoculation, and their interaction (Table 1). Compared with non-inoculated treatments, inoculation increases the concentration of leaf and root P under different soil water contents, while drought stress decreases the concentration of stem P for both inoculated and non-inoculated treatments (Fig. 4). Compared with non-inoculated treatments, inoculation increases the concentrations of leaf Ca and root Mg under drought stress, while drought stress decreases the concentration of leaf Ca and increases that of root Mg for both non-inoculated and inoculated treatments (Fig. 4).

3.4 Micronutrient Concentrations

The concentration of Zn in all tissues, leaf Mn, and root Cu is significantly affected by drought stress, inoculation, and their interaction (Table 1). Drought stress decreases the concentrations of leaf Mn and Zn and root Cu, while inoculation increases the concentrations of leaf Mn and

root Cu regardless of whether the plants were subjected to drought stress treatment (Fig. 5). Drought stress increases the concentration of stem Zn, while inoculation decreases the concentration of stem Zn regardless of drought stress treatment (Fig. 5).

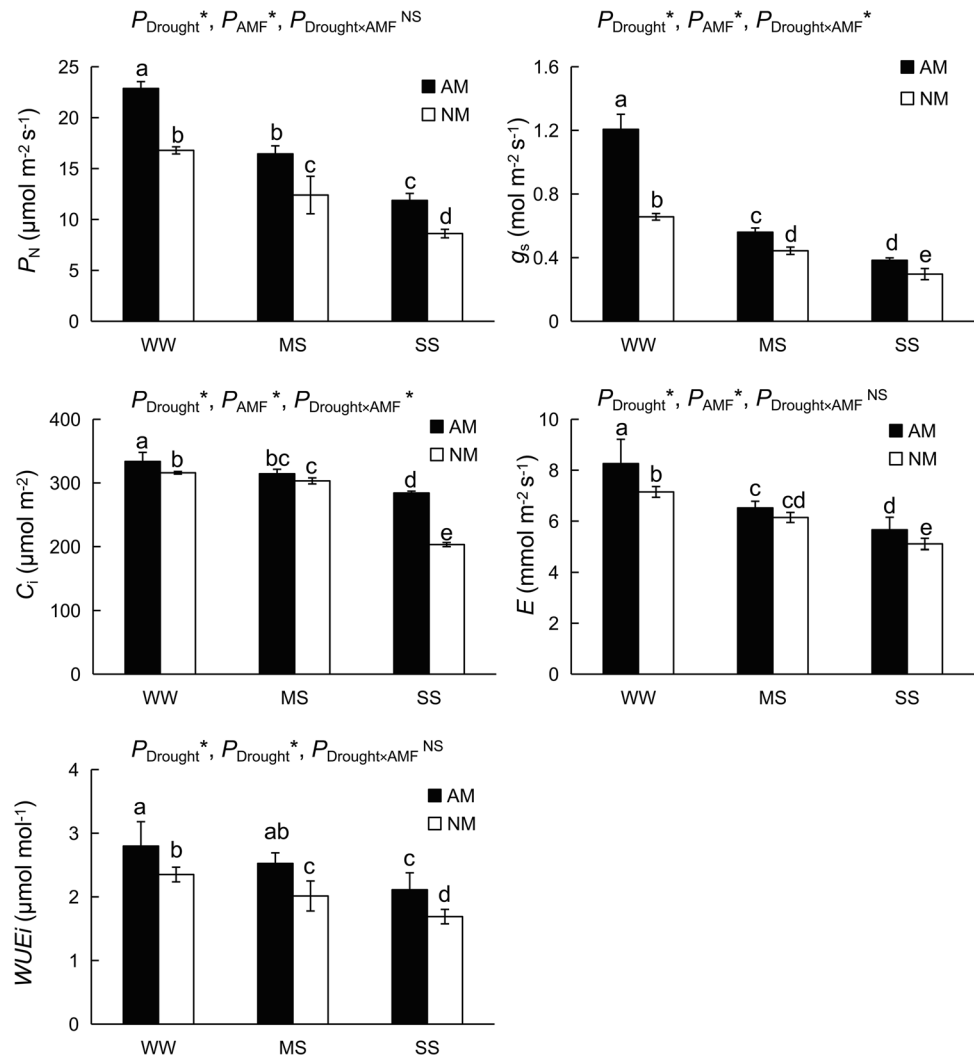
3.5 Macronutrient Contents

The contents of P and Ca in leaves and roots and Mg in roots are significantly affected by drought stress, inoculation, and their interaction (Table 2). Drought stress decreases the contents of P and Ca in leaves and roots, while inoculation increases the contents of P and Ca in leaves and roots under drought stress treatment (Table 3).

3.6 Micronutrient Contents

The contents of Cu, Fe, and Mn in roots and Mn in leaves are significantly affected by drought stress, inoculation, and their interaction (Table 2). Drought treatment and AM treatments had significant effects on the contents of Zn, Cu, and Fe in leaves. Drought stress decreased the contents of Cu,

Fig. 3 Effect of AM fungus and drought conditions on gas exchange. P_N , net photosynthesis; C_i , intercellular CO_2 concentration; g_s , stomatal conductance, E , transpiration rate, WUE_i , intrinsic water use efficiency; WW, well-watered; MS, mildly stressed; SS, severely stressed; AM, inoculated with *Rhizophagus irregularis*; NM, non-mycorrhizal; AMF, AM treatments; * $P \leq 0.05$; NS, not significant. Values with different letters indicate significant differences (Duncan's test $P = 0.05$, $n = 4$)



Fe, and Mn in leaves and roots, and the content of leaf Zn, while inoculation increased the contents of leaf Cu, Fe, and Zn and the root Fe and Mn contents under well-watered and mild drought stress conditions. Inoculation significantly increases the contents of leaf Mn and root Cu regardless of drought stress treatment (Table 4).

3.7 Nutrient Distribution

The distribution of K, Ca, and Cu occurred mostly in stems, whereas N, P, Mg, and Zn were distributed more in the leaves. Fe is primarily distributed in the roots (Fig. 6).

Under severe drought stress, inoculation decreased the distribution of N, P, K, and Mg in leaves and the distribution of K, Ca, Mn, and Zn in roots, and increased the distribution of N, P, K, Mg, Ca, Zn, and Mn in stems. Under well-watered and mild drought stress conditions, inoculation significantly increases the distribution of Mn and Zn in leaves and decreases the distribution of Cu and Mn in stems (Fig. 6). Drought stress significantly decreases the

distribution of Cu in roots for both inoculated and non-inoculated treatments, while inoculation increases the distribution of Cu in roots under the different water regimes compared with non-inoculated treatments (Fig. 6).

3.8 Principal Components Analysis and Correlation Coefficients of Nutrients

Principal components PC1 and PC2 together explain 91.6% of the variance (Fig. 7). The principal components analysis indicates that under well-watered and severely stressed conditions, inoculation significantly affected the absorption of nutrients, more under well-watered than under severely stressed (Fig. 7). Drought stress had a significant impact on the absorption of nutrients for both inoculated and non-inoculated treatments, and it had a greater effect on the absorption of nutrients in inoculated than non-inoculated plants (Fig. 7).

The results of a correlation analysis indicated that the growth parameters and gas exchange parameters are

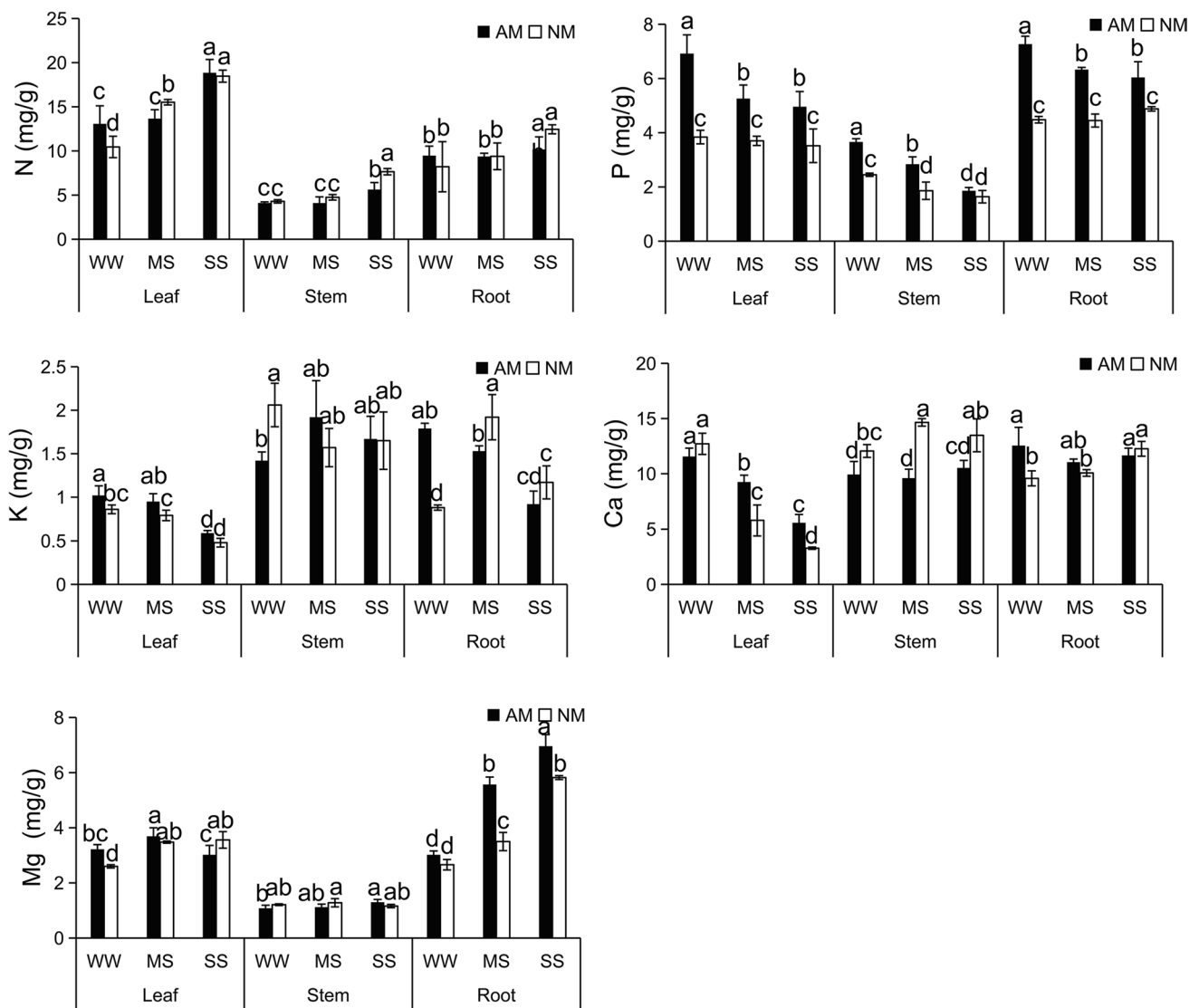


Fig. 4 Effect of AM fungus and drought condition on the concentration of macronutrient (N, P, K, Ca, Mg). WW, well-watered; MS, mildly stressed; SS, severely stressed; AM, inoculated with *Rhizophagus irregularis*; NM, non-mycorrhizal. Values with different letters indicate significant differences (Duncan's test $P=0.05$, $n=4$)

positively correlated with the concentrations of leaf P, K, Ca, Fe, Mn, Cu, and Zn and negatively correlate with the concentration of leaf N ($P < 0.05$, Table 5).

4 Discussion

Poplars are widely planted to meet various demands (Chen et al. 2017) and require a large supply of water and nutrients (Goehing et al. 2019). AMF rely on the lipid from host plants to complete their life span, and they supply mineral nutrients and water for exchange (Jiang et al. 2017). In this symbiotic relationship, both partners control the trade

(Hu et al. 2017). In this study, the degree of AM colonization of the roots of plants inoculated with *R. irregularis* exceeded 70%. This was observed in previous studies where *P. canadensis* 'Neva' could form symbiosis with AMF (Wu et al. 2017b). To control the loss of photosynthates that AM fungi demand, it has been suggested to decrease the colonization of plants under drought stress (Wang et al. 2017). The symbiosis established with the AMF increased plant height, stem diameter, and biomass, and the interaction between *P. canadensis* 'Neva' and *R. irregularis* has been documented in experiments (Wu et al. 2017b). Mycorrhizal *P. trichocarpa* showed improved growth (De Oliveira et al. 2019). Consistent with previous studies on poplar (Wu

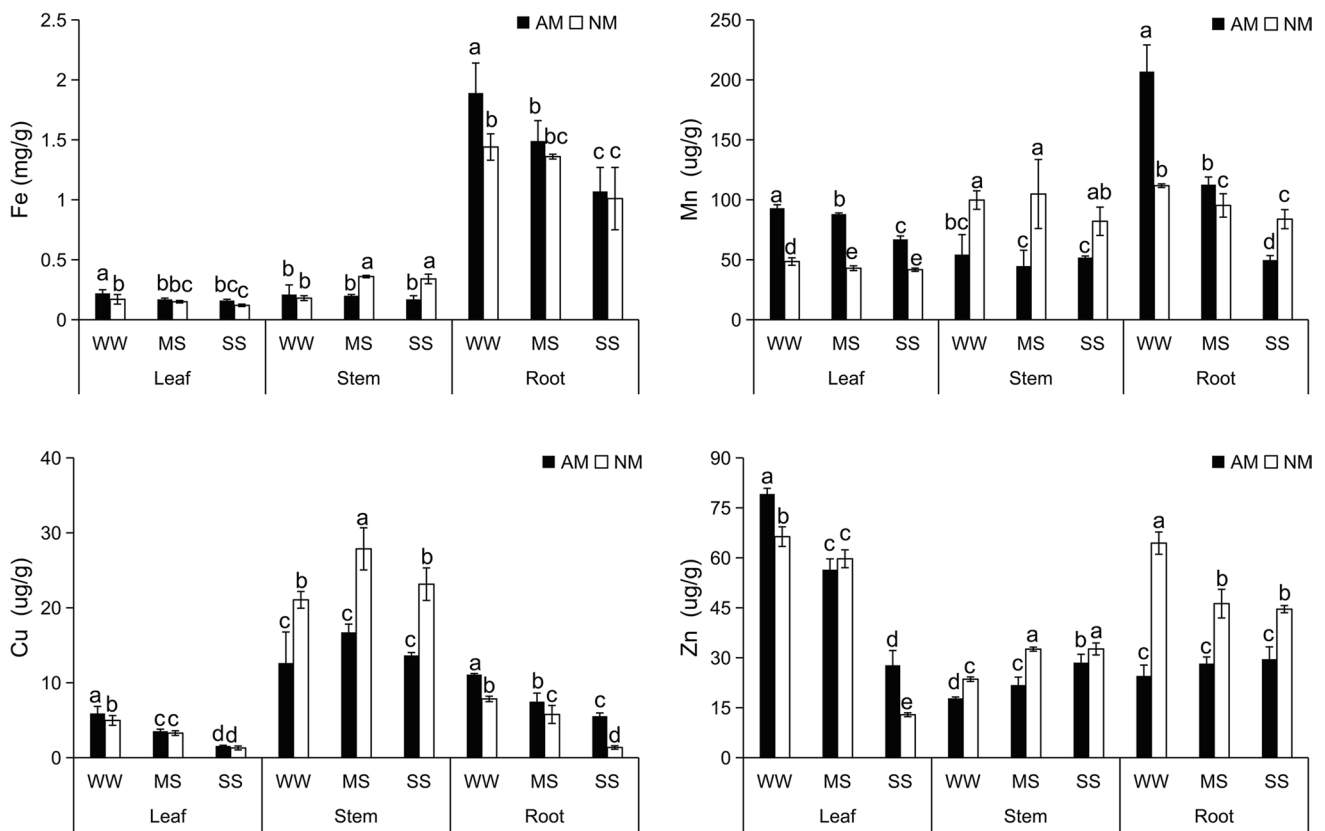


Fig. 5 Effect of AM fungus and drought conditions on the concentrations of micronutrients (Fe, Mn, Cu, Zn). WW, well-water; MS, mildly stressed; SS, severely stressed; AM, inoculated with *Rhizoph-*

agus irregularis; NM, non-mycorrhizal. Values with different letters indicate significant differences (Duncan's test $P=0.05$, $n=4$)

et al. 2017b), inoculation increased the parameters of gas exchange and photosynthesis, suggesting that mycorrhizal plants had a higher photosynthetic capacity.

Under drought stress, the concentrations of leaf Ca, Mn, and Zn and stem P diminished, whereas there were no changes in nutrient concentration in the roots, suggesting a notable decline in nutrient transportation from the below-ground to aboveground plant tissues under drought stress. Moreover, the percentage of distribution of P in the plant suggested a larger accumulation in roots but a decline of their transportation to leaves under drought stress.

The nutrient ions available to plants are dissolved in the soil solution. Thus, the absorption of nutrients by plants relies on water flow in the soil-root-shoot continuum, so that water and different nutrients always coexist in plant tissues (Keller 2020). The roots absorb soil solution that contains essential nutrients aided by leaf transpiration, which provides the necessary tension (Keller 2020).

Drought stress exerts adverse effects on plant nutrition. First, it causes a decrease in the growth rate of trees, particularly in the expansion rate of leaves (Zhang et al. 2018a, b). The reason for this is thought to be owing to an increase in the down-regulation effect on nutrient uptake. Secondly,

the water deficit has a negative impact on the availability of nutrients around the root. Third, it decreases stomatal conductance, which results in a lower leaf internal CO_2 concentration and photosynthetic rate, transpiration rate, and mass flow of nutrients among others.

Under well-watered and severe drought stress conditions, the inoculation of poplars with *R. irregularis* could have significantly affected the absorption of nutrients other than P, while the AMF apparently increased P concentration and contents in the leaves and roots, suggesting that *R. irregularis* can promote the absorption of P (Hu et al. 2017). Phosphorus is vital for plants because of its key role in signal transduction pathways and the structural composition of nucleic acids and phospholipids, and because it is a significant factor in energy transfer (Ramos-Artuso et al. 2019). Both P mineralization and mobility are generally constrained by many environmental conditions, such as drought (Goll et al. 2018). In addition, P uptake is affected by the water deficit, which can cause an inhibition of root growth (Zhang et al. 2018a, b). In fact, there are several adaptive strategies for plants to respond to low availability of P in soil. For instance, in order to increase the acquisition of P, the plant allocates more carbon to the root (Hu et al. 2017)

Table 2 A two-way ANOVA for the effects of drought, *Rhizophagus irregularis* inoculation, and their interaction on nutrient content of *Populus × canadensis* ‘Neva’

Index	Drought		AMF		Drought × AMF	
	F	P	F	P	F	P
Leaf N contents	2.65	0.11 ns	8.99	0.01*	2.25	0.15 ns
Stem N contents	35.43	0.00**	56.76	0.00**	17.00	0.00**
Root N contents	2.56	0.12 ns	12.09	0.00**	1.34	0.30 ns
Leaf P contents	72.79	0.00**	118.49	0.00**	15.49	0.00**
Stem P contents	212.21	0.00**	445.12	0.00**	3.75	0.05 ns
Root P contents	63.89	0.00**	133.81	0.00**	9.87	0.00**
Leaf K contents	56.42	0.00**	14.60	0.00**	1.94	0.19 ns
Stem K contents	0.18	0.84 ns	24.13	0.00**	14.37	0.00**
Root K contents	31.28	0.00**	41.56	0.00**	30.64	0.00**
Leaf Ca contents	77.66	0.00**	10.70	0.00**	4.08	0.04*
Stem Ca contents	21.97	0.00**	23.67	0.00**	31.08	0.00**
Root Ca contents	49.90	0.00**	60.41	0.00**	5.85	0.02*
Leaf Mg contents	26.04	0.00**	14.68	0.00**	7.52	0.00**
Stem Mg contents	9.20	0.00**	67.99	0.00**	24.86	0.00**
Root Mg contents	5.29	0.02*	104.17	0.00**	6.41	0.01*
Leaf Cu contents	107.98	0.00**	13.10	0.00**	2.65	0.11 ns
Stem Cu content	22.83	0.00**	0.55	0.47 ns	15.36	0.00**
Root Cu contents	163.95	0.00**	103.27	0.00**	6.81	0.01*
Leaf Mn contents	62.74	0.00**	167.09	0.00**	17.02	0.00**
Stem Mn contents	10.31	0.00**	3.42	0.09 ns	8.91	0.00**
Root Mn contents	115.90	0.00**	55.20	0.00**	31.09	0.00**
Leaf Fe contents	41.46	0.00**	20.49	0.00**	2.00	0.18 ns
Stem Fe contents	5.34	0.02*	1.70	0.22 ns	4.83	0.03*
Root Fe contents	76.66	0.00**	38.39	0.00**	5.35	0.02*
Leaf Zn contents	166.33	0.00**	24.22	0.00**	2.16	0.16 ns
Stem Zn contents	1.65	0.23 ns	40.47	0.00**	62.13	0.00**
Root Zn contents	70.75	0.00**	50.61	0.00**	27.27	0.00**

AMF, AM treatment; * $P \leq 0.05$, ** $P \leq 0.01$, ns, non-significant

and establishes mycorrhizal symbiosis, whose extended extraradical mycelia supplement the function of plant roots (Brundrett and Tedersoo 2018).

Under the drought stress treatments, inoculation with *R. irregularis* increased Ca concentration and contents in leaves. Thus, we considered that the diffusible molecules released by AMF can cause changes in the Ca contents in plant cells (Sujkowska-Rybkowska and Znojek 2018), transmitting drought signals to plants and causing a series of physiological changes to further resist the arid environment (Mbengue et al. 2020). Drought activates calcium ion channels located on the plasma membrane of the cell to generate specific calcium signals in the cytoplasm. Signals mediated by Ca^{2+} could act as core sensors and regulators in multiple adaptive and developmental aspects of plant metabolism (Bredow and Monaghan 2019). Calcium has been shown to promote the ability of leaves and their cellular membranes to preserve water, so as to effectively alleviate plant hydropenia under drought stress (Khan et al. 2017).

In this experiment, mycorrhization increased the concentration and contents of Mn in leaves, and the proportion of Mn transferred to the leaves under well-watered and mild drought stress. This was associated with an increase in the photosynthetic capacity in the inoculated plants, which is to be expected, because Mn is a component element in the water-splitting system of photosystem II and supplies essential electrons for photosynthesis in the thylakoid membranes (Cao et al. 2018). Recently, increasing numbers of studies have reported that Mn takes part in redox processes and could be an activator or cofactor of a variety of enzymes, including those needed for light-induced water oxidation in photosystem II (Lubitz et al. 2019).

The inoculation of poplars with *R. irregularis* significantly increased the concentration and contents of root Cu and the distribution of Cu in roots. The results might suggest that the biosorption of plant root cell wall and extracellular secretions produced by AMF could change the availability of Cu in the rhizosphere, thereby reducing the transmission

Table 3 Effects of drought conditions and *Rhizophagus irregularis* on the contents of macronutrients

Part		N(mg)	P(mg)	K(mg)	Ca(mg)	Mg(mg)
Leaf	WWAM	367.55 ± 32.46a	195.26 ± 16.37a	29.22 ± 5.72a	328.66 ± 50.48a	91.16 ± 7.32a
	WWNM	261.01 ± 20.59c	96.19 ± 8.16c	21.63 ± 2.38b	318.89 ± 34.89a	65.14 ± 2.76b
	MSAM	349.04 ± 66.63ab	133.06 ± 9.91b	24.16 ± 4.76ab	236.85 ± 47.48b	93.51 ± 10.28a
	MSNM	298.600 ± 50.51abc	71.24 ± 11.97de	15.24 ± 2.18c	113.89 ± 42.10c	66.91 ± 11.17b
	SSAM	279.57 ± 16.45bc	74.03 ± 12.50d	8.75 ± 0.97d	82.09 ± 2.37c	45.29 ± 9.08c
	SSNM	269.22 ± 24.65c	51.52 ± 10.93e	7.04 ± 1.21d	47.87 ± 4.4c	51.91 ± 7.63bc
Stem	WWAM	225.10 ± 6.64b	2002.31 ± 78.19a	77.60 ± 5.20a	544.85 ± 76.57a	59.66 ± 8.38ab
	WWNM	191.23 ± 12.04bc	1091.51 ± 50.8c	90.45 ± 9.00a	536.28 ± 29.63a	53.69 ± 1.46b
	MSAM	200.67 ± 34.97bc	1387.44 ± 108.02b	93.88 ± 20.32a	468.60 ± 30.67a	54.72 ± 6.49b
	MSNM	163.53 ± 15.34c	637.24 ± 91.00d	54.10 ± 9.06b	502.81 ± 4.71a	43.99 ± 6.41c
	SSAM	287.85 ± 34.89a	956.25 ± 82.49c	85.80 ± 1.00a	539.73 ± 40.70a	66.41 ± 4.16a
	SSNM	123.66 ± 7.71d	288.13 ± 33.32e	28.80 ± 5.25c	236.03 ± 21.00b	20.31 ± 1.03d
Root	WWAM	202.65 ± 18.62a	156.64 ± 16.58a	38.47 ± 4.33a	268.91 ± 35.12a	64.78 ± 6.40c
	WWNM	140.04 ± 47.19bc	76.64 ± 2.18c	15.02 ± 0.73c	163.75 ± 8.38bc	45.57 ± 4.20d
	MSAM	155.16 ± 16.29b	104.60 ± 7.40b	25.33 ± 1.29b	182.65 ± 12.75b	92.23 ± 10.92a
	MSNM	118.54 ± 15.29bc	56.43 ± 4.27d	24.36 ± 3.89b	127.53 ± 4.43 cd	44.26 ± 2.44d
	SSAM	114.43 ± 8.54bc	68.84 ± 12.51 cd	10.55 ± 2.72 cd	131.95 ± 11.87d	78.67 ± 4.06b
	SSNM	96.57 ± 16.01c	38.00 ± 7.60e	9.08 ± 2.22d	95.20 ± 17.35e	45.39 ± 9.50d

WW, well-watered; MS, mildly stressed; SS, severely stressed; AM, inoculated with *Rhizophagus irregularis*; NM, non-mycorrhizal. Values with different letters indicated a significant difference (Duncan's test $P=0.05$, $n=4$)

to the shoot, as previously shown by Sun et al. (2019). Copper is also necessary for redox systems and serves as an activator of many enzymes, primarily those required for superoxide radical detoxification and lignin synthesis (Ishka and Vatamaniuk 2020).

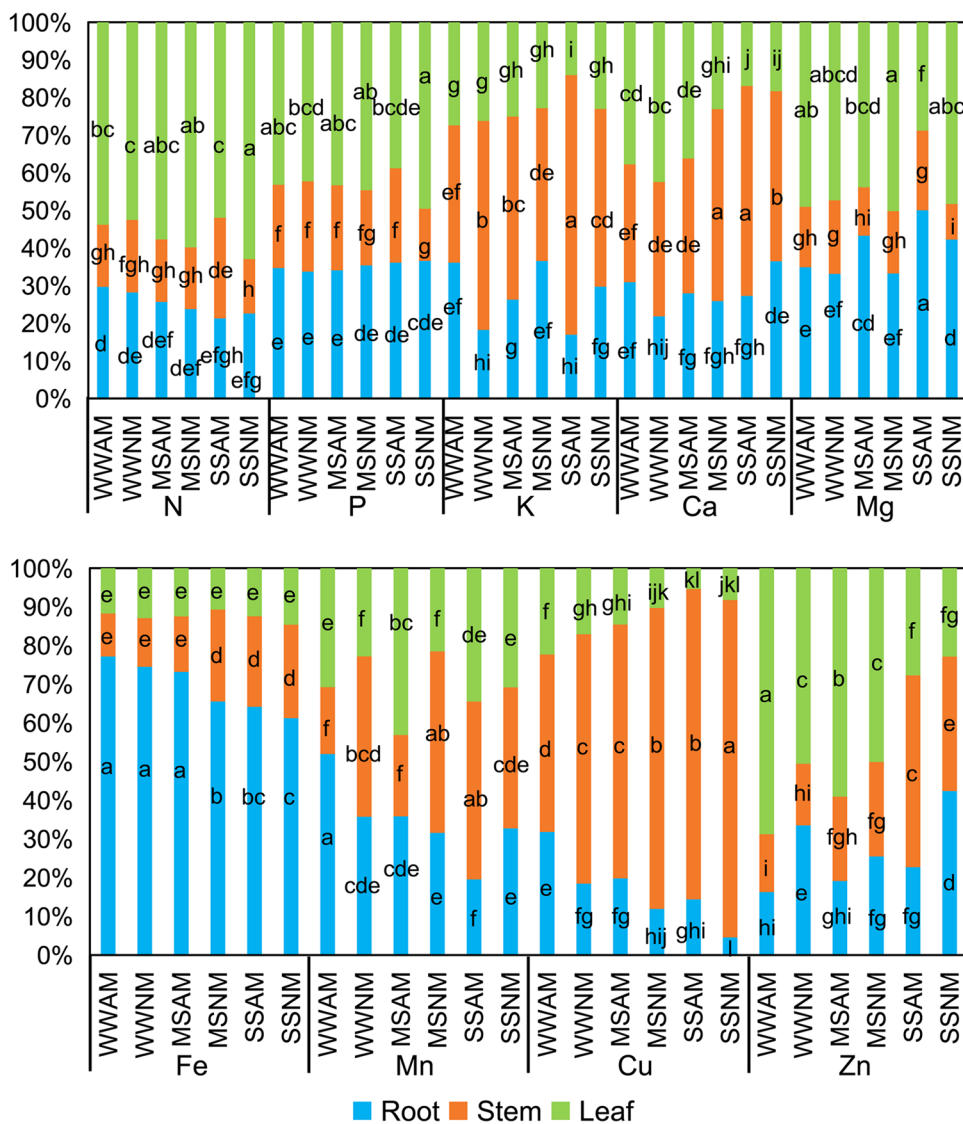
In this study, the contents and distribution of Mg were higher in leaves, supporting the concept that Mg is easily transferred to leaves and engages in photosynthesis (Geng et al. 2021). In most cases, Mg plays an important role in metabolic processes by activating numerous enzymes. For

Table 4 Effects of drought conditions and *Rhizophagus irregularis* on the contents of micronutrients

Part		Fe(mg)	Mn(μg)	Cu(μg)	Zn(μg)
Leaf	WWAM	6.18 ± 1.07a	2633.62 ± 219.31a	167.04 ± 25.32a	2241.90 ± 176.84a
	WWNM	4.27 ± 0.66b	1218.51 ± 149.88c	124.00 ± 10.63b	1660.61 ± 64.93b
	MSAM	4.17 ± 0.55b	2242.99 ± 315.75b	90.76 ± 18.99c	1444.83 ± 282.43b
	MSNM	2.81 ± 0.44c	822.04 ± 101.15de	63.03 ± 12.01d	1146.98 ± 183.57c
	SSAM	2.36 ± 0.22c	996.33 ± 62.71 cd	23.45 ± 2.69c	409.12 ± 24.00d
	SSNM	1.82 ± 0.11c	607.43 ± 48.04e	19.13 ± 4.99d	188.06 ± 19.37d
Stem	WWAM	11.71 ± 4.33ab	2962.80 ± 989.50bc	686.57 ± 198.06b	976.04 ± 16.85b
	WWNM	8.06 ± 1.18abc	4431.32 ± 210.67a	935.88 ± 42.71a	1047.07 ± 12.03b
	MSAM	9.53 ± 0.53abc	2187.45 ± 648.19 cd	816.88 ± 39.42ab	1066.72 ± 129.69b
	MSNM	12.34 ± 0.55a	3586.44 ± 941.36ab	955.62 ± 69.78a	1118.33 ± 17.76b
	SSAM	8.73 ± 1.31abc	2658.23 ± 101.25bc	699.57 ± 6.38b	1464.96 ± 159.74a
	SSNM	5.99 ± 0.59c	1436.93 ± 186.25d	405.37 ± 28.90c	572.14 ± 29.81c
Root	WWAM	40.70 ± 6.75a	4450.78 ± 667.04a	238.25 ± 21.99a	530.69 ± 111.25b
	WWNM	24.64 ± 1.48b	1911.15 ± 55.38b	134.08 ± 4.31b	1101.12 ± 51.10a
	MSAM	24.51 ± 1.43b	1865.20 ± 217.23b	123.44 ± 20.50b	468.23 ± 62.68bc
	MSNM	17.22 ± 0.94c	1207.65 ± 139.74c	73.25 ± 16.63c	584.12 ± 30.97b
	SSAM	12.18 ± 2.83 cd	565.76 ± 89.13d	62.77 ± 5.64c	335.60 ± 52.54d
	SSNM	7.63 ± 1.41d	645.70 ± 74.09d	10.60 ± 2.87d	348.90 ± 79.86 cd

WW, well-watered; MS, mildly stressed; SS, severely stressed; AM, inoculated with *Rhizophagus irregularis*; NM, non-mycorrhizal. Values with different letters indicated a significant difference (Duncan's test $P=0.05$, $n=4$)

Fig. 6 Effect of AM fungus and drought conditions on N, P, K, Ca, Mg, Fe, Mn, Cu, and Zn distribution percentage in different plant parts of poplar seedlings. WW, well-watered; MS, mildly stressed; SS, severely stressed; AM, inoculated with *Rhizophagus irregularis*; NM, non-mycorrhizal. Values with different letters indicate significant differences (Duncan’s test $P=0.05$, $n=4$)



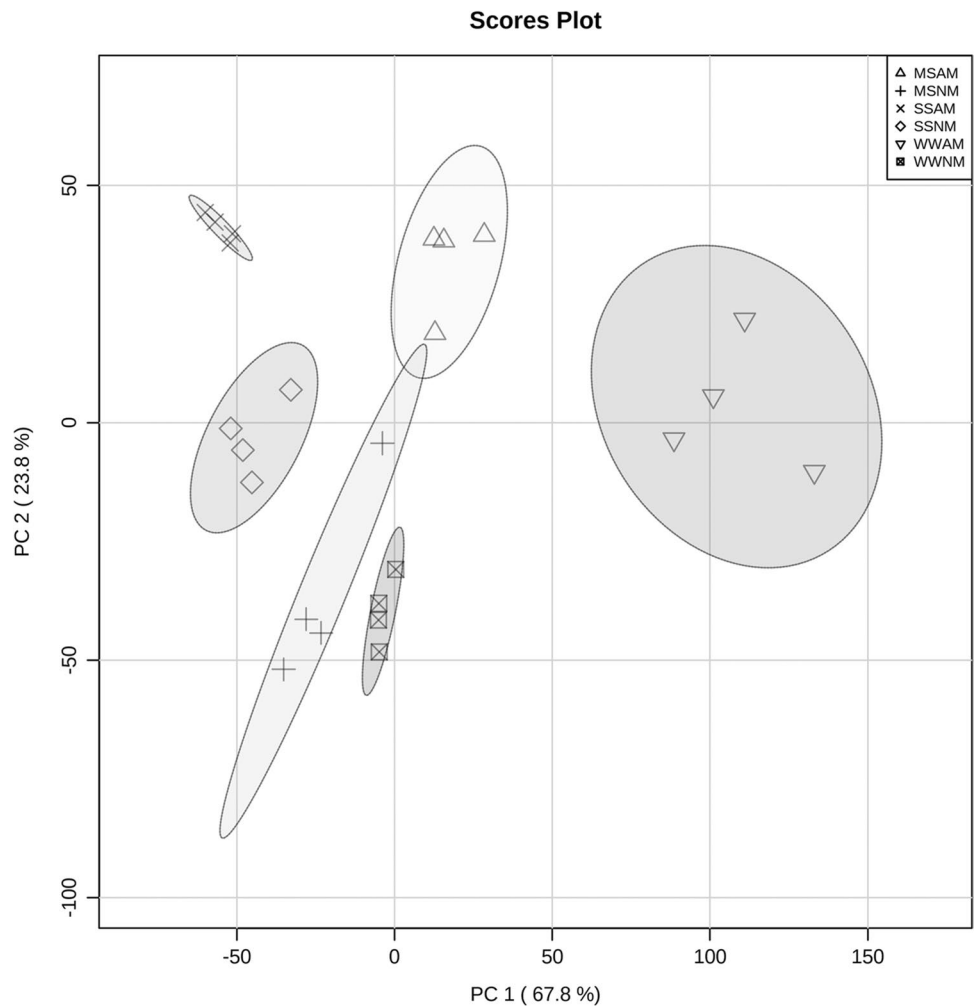
instance, RUBISCO, a Mg-activated enzyme, could participate in photosynthesis and other biological processes (Rodrigues et al. 2021). Under drought stress, inoculated plants accumulated less Mg in leaves and more in the roots. These results showed that the Mg in leaves was sufficient for photosynthesis, and AMF maintained needless Mg in the roots, reducing the energy required for mineral nutrient transport (Lopes et al. 2020).

The distribution of iron was higher in the roots, and our results support the concept that Fe may be tightly bound to root cells, as previously indicated (Sterckeman et al. 2021). In this study, inoculation with *R. irregularis* increased the contents and distribution of Fe in roots under mild drought stress. These results are consistent with a previous study in which *Funneliformis mosseae* enhanced the uptake of Fe to maize plants that were grown under drought stress (Bahraminia et al. 2020).

Drought stress had a significant influence on the absorption of Zn, decreasing its contents and distribution in the leaves, while inoculation increased them. Zinc is essential to the membrane integrity, detoxification of superoxide radicals, and the synthesis of the phytohormone IAA and proteins (Nakandalage and Seneweera 2018). It has been demonstrated that Zn can be transferred by AMF external mycelia (Upadhayay et al. 2019). Our results showed that AMF could absorb and deliver Zn to the host, thereby improving plant Zn nutrition (Ruytinx et al. 2019).

Nutrient transport in plants is a very complex process, which involves many transporters. Nutrient transporters play an important role in nutrient absorption and signal transduction (Sun et al. 2020). Studies showed that one transporter can simultaneously transport multiple nutrient elements. For example, PtrZIP gene is expressed

Fig. 7 The principal component analysis of nutrients in leaves, stems, and roots of poplar cuttings. WW, well-watered; MS, mildly stressed; SS, severely stressed; AM, inoculated with *Rhizophagus irregularis*; NM, non-mycorrhizal. PC1, principal component 1; PC2, principal component 2



not only under Zn, Fe, Cu, and Mn deficiency or excess stress, but also under cadmium (Cd) and lead (Pb) excess stress (Zhang et al. 2017). Moreover, the genes involved in the absorption, transport, and distribution of nutrient

are also different. Therefore, it is difficult to select the appropriate transporter gene for research. However, research on nutrient transporters is very meaningful and can be focused on in the future.

Table 5 Correlation coefficients between the gas exchange parameters and nutrient concentrations in the leaves of poplar

	N	P	K	Ca	Mg	Fe	Mn	Cu	Zn
Plant height	-0.768**	0.650**	0.907**	0.884**	-0.239	0.775**	0.641**	0.930**	0.932**
Stem diameter	-0.827**	0.537**	0.851**	0.907**	-0.399	0.656**	0.556**	0.922**	0.909**
Dry weight of stem	-0.424*	0.719**	0.661**	0.673**	-0.322	0.671**	0.778**	0.562**	0.623**
Dry weight of root	-0.754**	0.669**	0.904**	0.887**	-0.257	0.783**	0.689**	0.874**	0.872**
P_N	-0.685**	0.764**	0.860**	0.834**	-0.219	0.802**	0.723**	0.883**	0.855**
g_s	-0.792**	0.499*	0.767**	0.870**	-0.168	0.586**	0.597**	0.778**	0.687**
C_i	-0.674**	0.552**	0.856**	0.790**	-0.279	0.690**	0.566**	0.764**	0.899**
E	-0.691**	0.615**	0.749**	0.788**	-0.21	0.685**	0.612**	0.913**	0.841**
WUE_i	-0.561**	0.761**	0.822**	0.727**	-0.18	0.762**	0.713**	0.686**	0.697**

** $P \leq 0.01$. P_N , net photosynthesis; C_i , intercellular CO₂ concentration; g_s , stomatal conductance; E , transpiration rate; WUE_i , intrinsic water use efficiency

5 Conclusions

In summary, this indicated that arbuscular mycorrhizal fungi promote the growth and gas exchange parameters of poplar under drought stress. Moreover, the gas exchange parameters positively correlated with the concentrations of leaf P, K, Ca, Fe, Mn, Cu, and Zn. Under severe drought stress, inoculation decreased the distribution of N, P, K, and Mg in leaves and the distribution of K, Ca, Mn, and Zn in the roots and increased the distribution of N, P, K, Mg, Ca, Zn, and Mn in stems. The results demonstrated that nutrient absorption and changes in the distribution of nutrients were enhanced in the mycorrhizal poplar cuttings, which resulted in the enhanced photosynthetic capacity of poplar, plant growth, and limited biomass loss during drought stress compared with the non-mycorrhizal cuttings, leading to an improvement in the drought resistance of poplar.

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