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The effect of drought stress on *Pinellia ternata* in terms of physiology and aquaporin genes after Arbuscular mycorrhizal fungal inoculation

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Summary

Pinellia ternata (*P. ternata*) is a traditional Chinese herbal medicine. Arbuscular mycorrhizal fungi (AMF) establish symbiosis with plants, which is essential in improving mineral nutrient acquisition and drought resistance of host plants. This study used the medicinal plant *P. ternata* as the experimental material to investigate the similarities and differences in photosynthesis, osmotic regulation, and antioxidant activity between arbuscular mycorrhizal and non-arbuscular mycorrhizal plants under drought stress. The results showed that AMF inoculation could significantly increase the photosynthetic rate (*Pn*), stomatal conductance (*Gs*), and transpiration rate (*Tr*) of *P. ternata*. Under drought stress, *P. ternata* adapted to drought by accumulating osmotic regulatory substances such as proline and soluble proteins and increasing chlorophyll content. In addition, Mycorrhizal *P. ternata* also exhibited high activities of peroxidase, superoxide dismutase, and catalase under drought conditions, improving the response of the antioxidant system. AMF could promote the growth and development of *P. ternata* under drought stress. Mycorrhization upregulated the expression of *Pf*TIP, NIP, and PIP genes under drought stress. AMF can alleviate drought stress-induced damage by regulating photosynthetic capacity, osmosis, antioxidant activities, and aquaporin gene expression. Our study highlights the effect of AMF on *P. ternata* under drought stress by mediating physiological and biochemical activities.

Keywords: *Pinellia ternate*; Arbuscular mycorrhizal fungi; Drought stress; Physiology; Aquaporin

Introduction

Pinellia ternata (*P. ternata*) is a dry tuber of *P. ternata* (Thunb.) Breit. in the *Araceae* family and the Pinellia genus. *P. ternata*, with the first record in *Sheng Nong's herbal classic* (Mao and He, 2020), has a long history of utilization in medicine and is one of the most popular Chinese medicinal herbs. It consists of various chemical components such as alkaloids, flavonoids, organic acids, volatile oils, amino acids, etc. (Bai et al., 2022). Its pharmacological effects encompass antitussive, antifungal, antiemetic, anti-tumor, and anticonvulsant properties (Ji et al., 2014). Adenosine in *P. ternata* alkaloids and succinic acid in organic acids reduce lipofuscin and inhibit the expression of genes encoding aging β-galactosidase (Tang et al., 2020). The baicalein, β-sitosterol, and stigmasterol in *P. ternata-Semen coicis* decoction can be used to treat insomnia, especially in those with difficulty falling asleep and maintaining sleep (Chen et al., 2023). *P. ternata* has been documented to possesses pharmacological functions of anti-depression, wound-healing, anti-coughing, and anti-vomiting (Mao and He, 2020). However, the excessive collection of wild resources and environmental degradation result in increasingly compromised availability of *P. ternata* (Hang et al., 2023). The growth of *P. ternata* requires specific environmental conditions, and it is particularly susceptible to seedling lodging. It is important to note that rather than inevitable physiological phenomenon, lodged seedlings are a response to adverse environmental conditions such as high temperatures, drought, and intense light, which induce a state of dormancy (Zhang et al., 2004; Huang et al., 2019).

In nature, almost all living organisms do not exist independently and generally have symbiotic relationships (Brownlee et al., 1983). Plants forge mutualistic associations with specific strains of bacteria, actinomycetes, and fungi to create symbiotic relationships. Among mycorrhizal fungi, arbuscular mycorrhizal fungi (AMF) establish the predominant symbiotic connection with the roots of 72% of terrestrial plants (Wang et al., 2023). AMF offer vital ecological benefits to plants, particularly in enhancing their nutritional uptake and resilience to stress (Diao et al., 2021). AMF collaborate with host plants to create an extensive mycelial network within the soil that can boost the exchange of plant carbohydrates and soil nutrients for a mutually beneficial symbiosis (Gosling et al., 2006; Xia et al., 2022). Mycorrhizae-plant connection can mitigate the impacts of abiotic stresses, including drought, extreme temperatures, salinity, and heavy metals, by encouraging plant health and enhancing yields (Feng et al., 2020). Additionally, these symbiotic relationships bolster plants' resistance to biological stresses caused by microorganisms such as bacteria, fungi, and viruses, as well as nematodes and phytopathogens (Mathur et al., 2018; Dowarah et al., 2022). As indicated previously, AMF secretes glomalin into the soil to enhance the stability of soil aggregates via mycorrhizal extraradical mycelium, while also influencing the expression of genes that respond to stress (Cheng et al., 2021).

As one of the main abiotic stresses drought may produce negative impacts on normal growth, development and yields of plants (Cui et al., 2022). It can result in slowed cell division, reduced seedling growth, and disturb plant cell membrane integrity. Drought also interferes with essential physiological processes, such as respiration and photosynthesis, severely affecting overall physiological metabolism and yield in plants (Gosling et al., 2006; Praba et al., 2009; Kaushal, 2019). Notably, AMF can alleviate reverse drought-induced damages suffered by various plants (Balestrini and Lumini, 2018). With the establishment of mycorrhizal colonization within the root system, the existence of AMF provides plants with nutrient and water uptake through an extensive hyphal network in the soil rhizosphere. Consequently, it may benefit leaf gas exchange, activation of antioxidant defense systems, and maintenance of osmotic pressure across plant cells, which eventually nullify the antagonistic effects of external stresses (Wang et al., 2023; Abrar et al., 2024). Under drought stress, AMF significantly increase the biomass of strawberry by increasing photosynthesis rate, water content and utilization efficiency, antioxidant enzyme defense, and improving nutritional status (Moradtalab et al., 2019). LI et al. (2013) first

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cloned two aquaporin genes (AQPs), GintAQPF1 and GintAQPF2, from an arbuscular mycorrhizal fungus of Glomus intraradices, which facilitate the interpretation of the important role of AMF in plant drought resistance. Dong Huang et al. (HUANG et al., 2020) found that AMF exerted superior ability in balancing the distribution of light energy and increasing the content of antioxidant enzymes in drought resistance of apple plants to alleviate oxidative stress damage and hence mitigate the damage of drought on these plants.

In this study, AMF colonization experiment was conducted for *P. ternata* to uncover their roles in alleviating the impact of drought stress on the growth, physiology, and AQP expression of this medicinal herb. This study intends to explain the mechanism of AMF in drought resistance and lay a solid foundation for enhancing the tolerance of medicinal plants to drought stress.

Materials and methods

Experimental design and materials

The *P. ternata* tubers were planted in a flowerpot (17.5*23.5 *23.5 cm) containing 600 g of peat soil (PH5.0~6.0,0~5mm, sterility) in a greenhouse under natural light and temperature at the Shaanxi Province Traditional Chinese Medicine Resource Industrialization Provincial and Ministerial Collaborative Center. Each pot contains 10 tubers, and each treatment includes 5 pots. The four treatments were CK: non-colonization + well-watering, AM: colonization + well-watering; DA: drought stress + colonization; and DN: drought stress + non-colonization. A mixed microbial agent (30 g of *Funneliformis mosseae* and *Rhizophagus intraradices*; BENEAGRICULTURE BIOTECH, Guangdong) was inoculated in the soil and cultivated together for 30 days to form AMF. The watering volume and frequency were 100 mL every two days, with the natural drought method for treatment. Samples were harvested to measure physiological indicators after 7, 14, 21, and 28 days of natural drought.

AMF colonization measurement

Seedling roots harvested freshly from *P. ternata* were thoroughly cleaned and subjected to 0.05% trypan blue stain treatment. Then, these samples were washed and decolorized using a lactic acid-glycerol solution made up of lactic acid, glycerol, and distilled water in a 1:1:1 v/v/v ratio. Following this process, the roots were examined under a microscope. The root colonization rate was determined by calculating the percentage of root segments colonized by AMF in relation to the total number of observed root segments.

Determination of plant growth parameters and relative water content (RWC)

Plant growth parameters, measured by meter ruler or vernier caliper, included plant height, leaf length and width, and stem diameter. Fresh leaves were removed to weigh and recorded as fresh weight (FW). Afterwards, the turgid weight (TW) of the removed fresh leaves were measured by immersing leaves in distilled water-filled Petri dishes. The dry weight (DW) was obtained by drying these samples in oven.

RWC (%)=(FW-DW)/(TW-DW)×100%

Determination of chlorophyll concentration

After the collection of 0.1 g fresh leaf, samples in small pieces were processed by adding and soaking within 25 mL of 96% ethanol for 24 h in dark. The supernatant was obtained and subjected to measurement of the absorbance at 665 nm, 649 nm, and 470 nm using ultraviolet-visible spectrophotometer (Shimadzu UV 2600, Shimadzu, Kyoto, Japan). Chlorophyll concentration calculation adhered to formulas below:

Ca = 13.95 ×A665 nm-6.88 ×A649 nm

Cb = 24.96 ×A649 nm-7.32 ×A665 nm

Cx·c = (1000 ×A470 nm-2.05 ×Chl a-114.8 ×Chl b)/245

The content of each pigment ($mg \cdot g^{-1}$) = (C×Vt)/(FW × 1000)

where, C, Vt and FW respectively represent the chlorophyll concentration (mg L^{-1}), the total volume (mL) of the extract, and the fresh weight (g) of leaves.

Photosynthesis measurements

A portable gas exchange system (CIRAS-3, Lufthansa Scientific Instrument Co., Ltd.) was used for measurement at 9:00-11:00 am, including photosynthetic rate (*Pn*), transpiration rate (*Tr*), intercellular CO_2 concentration (*Ci*), stomatal conductance (*Gs*) and water use efficiency (*WUE*). After the stabilization of *Pn*, we then measured chlorophyll fluorescence parameters, *i.e.*, energy of PSII capture efficiency(*Fv*/*Fm*), Excitation energy of PSII Capture efficiency (*Fv'*/*Fm'*) effective quantum yield of PSII (*ΦPSII*), non-cyclic electron transfer efficiency (*ETR*), photochemical quenching (*qP* and *qL*), and non-photochemical quenching (*NPQ*).

Determination of physiological indexes

To extract enzymes, 0.5 g of fresh *P. ternata* leaf samples were ground using a mortar and pestle with 10 mL of a buffered solution comprising 50 mM phosphate brine (pH 7.8) along with 1% polyvinyl pyrrolidone (PVP). Following centrifugation at 4 °C and 12,000 rpm for 20 min, the supernatant was obtained for antioxidant enzyme assessment as outlined below.

The assessment of SOD activity involved a reaction mixture of 3.3 mL, which included 50 mM phosphate buffer (1.5 mL, pH 7.8); 100 μM EDTA-Na2, 130 mM methionine, 750 μM NBT, and 60 μM riboflavin (300 μL each); enzyme extraction buffer (100 μL); and distilled water (500 μL). After treatment in greenhouse incubator lighting for 20 min, the mixture was subjected to the measurement and reading of the absorbance at 560 nm.

CAT activity was asseesed in a 3 mL reaction mixture composed of 50 mM phosphate buffer (1 mL, pH 7.0), enzyme extraction buffer (100 μL), 200 mM H_2O_2 (200 μL), and distilled water (1.7 mL). Absorbance readings were taken at 240 nm following a 3-minute incubation. A Shimadzu UV 2600 spectrophotometer was utilized to perform the absorbance measurements.

The activities of SOD and CAT were obtained based on the formula described below:

(1) SOD activity ($u \cdot g^{-1}FW \cdot h^{-1}$) = [(Ac-At)×Vt×60]/(0.5×Ac×FW×Vs×t)

(2) CAT activity($U \cdot g^{-1}FW \cdot min^{-1}$) = (ΔA240×Vt)/(FW×Vs×0.1×t)

where, At is the absorbance of the sample in formula (1); Ac is the absorbance of control, t is reaction time (min), Vt is the total volume of enzyme solution (mL), and Vs is the volume of enzyme solution added during the reaction (mL) in both formulas (1) and (2); and ΔA240 is the decrease in absorbance in formula (2).

The assessment of soluble protein utilized the Coomassie Brilliant Blue method. Fresh samples of *P. ternata* leaves (0.1 g) were crushed in a mortar added with 4 mL of water using a pestle. The supernatant (0.1 mL) obtained by centrifugation (5,000 rpm, 10 min) was mixed with 0.9 mL of water and 5 mL of the test reagent for 2 min to measure at 595 nm. The calculation formula of soluble protein was:

Soluble protein ($mg \cdot g^{-1}$) = (C×Vt)/(FW×Vs×1000)

where, C is the standard curve value, Vt is the total volume of the extraction solution (mL), Vs is the amount of sample added during measurement (mL), and FW is the fresh weight.

Similar to that in the method of chlorophyll content, 0.1 g fresh leaf-derived veins were removed for subsequent experiments. The leaf fragments were then chopped into smaller sections, combined with 20 mL of water, and allowed to soak for 24 h. A conductivity

meter was employed for measurement. The calculation of relative electronic leakage (REL) was performed using the formula outlined below:

$REL(\%) = C1/C2 \times 100\%$

where, C1 is the measurement value before boiling to death, and C2 is the measurement value after boiling to death.

The measurement of glutathione (GSH), proline (Pro), soluble sugars (SS), and peroxidase (POD) was conducted utilizing kits A006-2-1, A107-1-1, A145-1-1, and A084–3-1 (Nanjing Jiancheng Bioengineering Institute, China), respectively. Corresponding readings were recorded at 405, 520, 620, and 420 nm, respectively, using Agilent BioTek Synergy H1 (USA). The quantities were computed according to the following formulas:

$GSH\ (\mu mol \cdot g^{-1}) = (At-Ab)/(As-Ab) \times Cs \times n \div (FW/Vt)$

$Pro\ (\mu g \cdot g^{-1}) = (At-Ab)/(As-Ab) \times Cs \times n \div (FW/Vt)$

$SS\ (\mu g \cdot g^{-1}) = (At-Ab)/(As-Ab) \times Cs \times n \div (FW/Vt)$

$POD\ (u \cdot g^{-1}FW) = (At-Ab)/[(12 \times d) \times V/Vt \div T \div FW/V \times 1000]$

where, At, Ab and As are the absorbance of the sample, distilled water, and standard, respectively; n is the dilution factor, FW is the fresh weight (g), Vt is the total volume of the extract (mL), and Cs is the concentration of the standard (20 $\mu mol \cdot L^{-1}$, 5 $\mu g \cdot mL^{-1}$, and 100$\mu g\ mL^{-1}$ for GSH, Pro, and SS).

Real-Time qPCR

The isolation of total RNA referred to the protocols described in the Plant RNA Kit (Beijing Tiangen, China). cDNA synthesis was carried out using the Fast Synthesis Kit for the first-strand cDNA (Beijing Tiangen, China). Gene-specific primers, shown in Tab. 1, were produced by Sangon (Shanghai, China). Real-time PCR utilized the 2×Q3 SYBR qPCR Master Mix (TOLOBIO, China). The qPCR assays were executed on a qTO WER3G device (Analytik Jena, Germany) in two steps: (1) a denaturation phase lasting 30 s at 95 °C, and (2) a 40-cycle program for amplification and quantification (10 s of denaturation at 95 °C, 30 s of annealing and elongation at 60 °C). The 18S ribosomal gene served as the internal control (Duan et al., 2019). Quantification of target mRNA levels was computed using the $2^{-\Delta\Delta CT}$ methodology.

Data analysis

Microsoft Excel 2021 and SPSS 26 were used for data organization and significance analysis (n=3, LSD method, $P<0.05$). The Wekemo Bioinformatics cloud was employed to analyze data of the orthogonal partial least-squares discrimination analysis (OPLS-DA) for various physiological indices. GraphPad Prism and Figdraw were utilized to generate graphs (Fig. 10 data standardization and plotting).

Tab. 1: Specific primer sequences of AQPs in *P. ternata*.

Genes	Primer sequence (5'→3')
PtNIP-1	F: ATACCCTTTCACACTTCCGTCACC
	R: TGGTCGGCGTCTCCTGTCTC
PtNIP-2	F: GAAGTGTCTCAACGCCGCAAAG
	R: TGATATACGCTGTCGGGCACATC
PtPIP-1	F: GCACACAGACGGACCCTCAC
	R: TTTAGACACGCACGAAACCATCAC
PtPIP-2	F: TGGAGGAGCAGCAGGGAGAG
	R: GAAGAGGAGGGTGGCGATGAAC
PtPIP-3	F: GGAGATGGACACGCAGAGATGAC
	R: CAGACAGAGACGGGGACCAATG
PtTIP-2	F: TCACAAGCGGAACAGAACAAATGG
	R: CGTTGGAATAATCTGCGTGGACATC
PtTIP-3	F: CTAGTAGGTTGCTGAGGTCGTCTG
	R: GCGGATCGGTGTAGTCCTTCG
PtTIP-5	F: ACGAAGAGCAGAGTGGAGATGAAC
	R: CCTTCGGCAGCTTCGGTGAC
PtTIP-6	F: GCCAATTAACCAGCAGAAGCAGAG
	R: GACGAAGATGAGCATGGAGATGAAC
Pt-18s	F: CGCATATAAATAAACGGAGGAA
	R: GACGCTTCTACAGACTACA

Results

AMF colonization and plant growth

Trypan blue staining allowed for the observation of AMF infection in the root system of *P. ternata* seedlings (Fig. 1). Seedlings lacking inoculation with AMF did not exhibit any signs of infection. In contrast, the roots of seedlings that had been inoculated with AMF for 30 days revealed a substantial presence of mycelium. Consequently, a strong symbiotic relationship was established between AMF and the root system of *P. ternata* seedlings. No colonization was observed in *P. ternata* plants in the absence of inoculation. Plants in the presence of inoculation had a AMF colonization rate of (47.76±5.35)% compared to CK (0%). The 30-day AMF inoculation increased the leaf length, plant height, and stem thickness of *P. ternata*, with an increase of 16.97%, 6.51%, 16.29% compared to CK (Fig. 2).

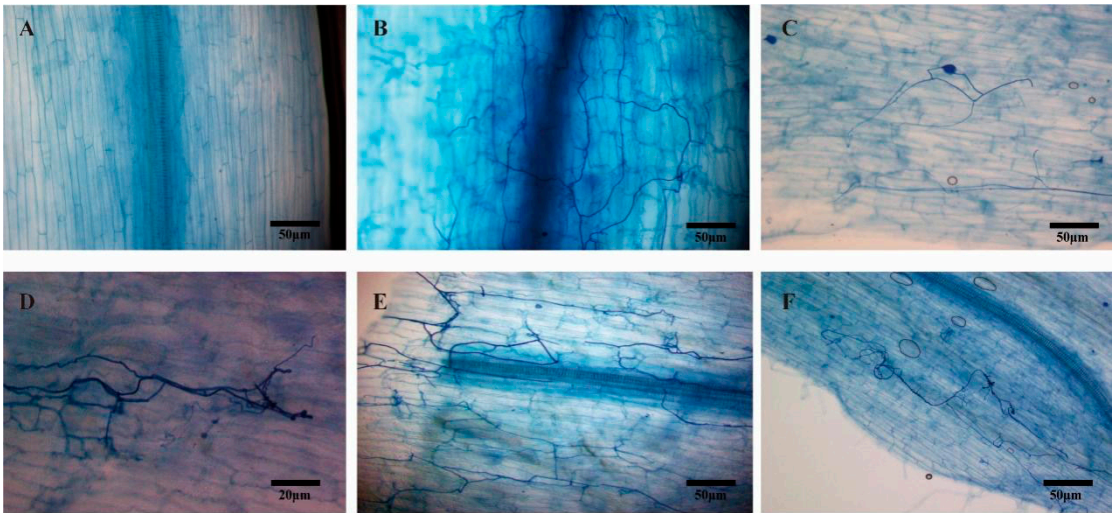

Fig. 1: (A) Roots of *P. ternata* without AMF inoculation; (B–F) Hyphae, vesicles, and arbuscules in roots of *P. ternata* after AMF infection

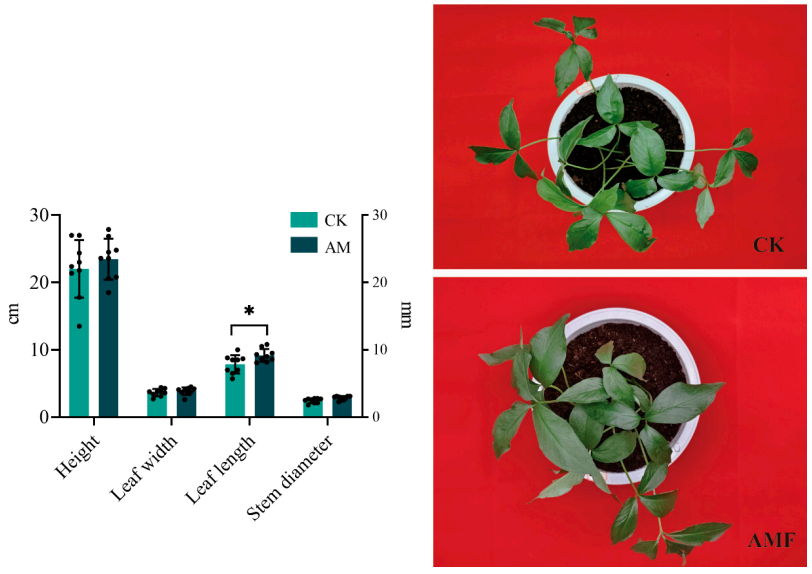

Fig. 2: Effect of 30-day AMF inoculation on plant growth

Effect of AMF treatments on RWC

Plants in DA group exhibited much higher RWC than that in DN group when subjected to drought stress. However, as the drought duration extended, the DA group began to show a decreasing trend. A notable difference was observed between groups after 14 days of drought treatment. Furthermore, the DN group reduced by 9.29% after 28 days of drought (Fig. 3).

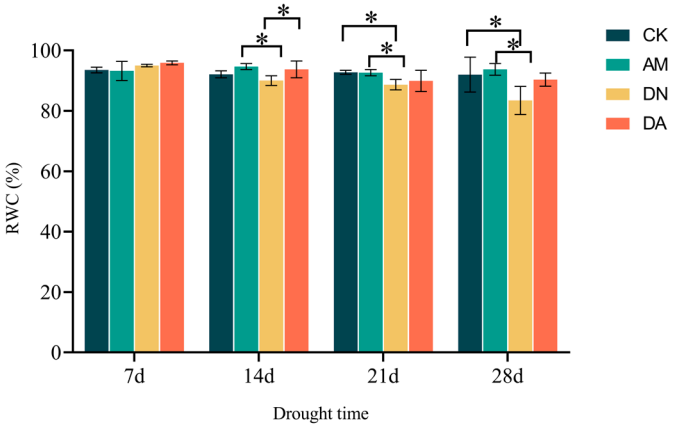

Fig. 3: Effect of AMF treatments on RWC. * $P<0.05$
Note: CK: non-colonization + well-watering, AM: colonization + well-watering; DA: drought stress + colonization; and DN: drought stress + non-colonization; RWC: relative water content.

Effect of AMF treatments on photosynthetic pigments

Contents of chlorophyll a, b, carotenoids (Car), and total chlorophyll decreased greatly after exposure to drought (Fig. 4). On the 21st day, AM group had increased contents of chlorophyll a, b, Car, and total chlorophyll compared to CK, with the increase of 35.31%, 26.43%, 39.84%, and 32.24%. Drought stress reduced the content of chlorophyll a, b, Car, and total chlorophyll in *P. ternata* leaves. Compared with CK, there were significant differences in chlorophyll a, b, Car, and total chlorophyll content during natural drought for 7, 14, 21, and 28 days (all $P<0.05$). After 28 days of drought, the contents of the four indices reached their lowest levels, decreasing by 46.49%, 35.01%, 45.48%, and 42.60%, respectively. Compared with DN group, DA group had significantly increased chlorophyll-a content by 7.40%, 23.69%, 23.80%, and 69.24%, respectively; chlorophyll b by 7.06%, 21.57%, 20.96%, and 45.76%; Car by 18.22%, 25.96%, 20.28%, and 52.48%; and total chlorophyll content by 7.26%, 22.96%, 22.80%, and 60.23%, respectively. As a result, AMF treatment can significantly increase chlorophyll content to resist damage caused by drought stress.

Effect of AMF treatments on gas exchange parameters

Inoculation with AMF increased *Pn*, *Gs*, and *Tr*. On 7d, the AM group achieved the highest *Pn* and *Tr*, which were 10.43% and 48.32% higher than the CK group, respectively. *Gs* reached its highest point on 21d, 51.01% higher. With the prolongation of drought time, *Pn*, *Gs*, and *Tr* showed decreasing trends, while the *WUE* increased first and then decreased. On 14d, *WUE* reached its highest value. After inoculation with AMF, the peak of *WUE* was delayed until 21d. Under drought stress, compared with the DN group, the DA group had significantly increased *Pn* by 14.91%, 21.85%, and 58%; *Gs* by 52.72%, 19.23%, 6.11%, and 45.83%; and *Tr* by 41.34%, 39.80%, 10.23%, and 38.60%, respectively(Tab. 2). AMF inoculation ameliorated drought stress-induced photosynthesis activity decrease.

Effect of AMF treatments on chlorophyll fluorescence

Fv'/Fm' and *qP* and *ΦPSII* were the lowest under drought treatment, while DA group was higher than the DN group. Under well-watering conditions, AMF inoculation had little effect on *Fv'/Fm'*, *ΦPSII*, and *ETR*. Compared with CK, drought treatment resulted in decreased *Fv/Fm*, *Fv'/Fm'*, *ΦPSII,* and *qP* to varying degrees. The *ΦPSII*, *qP*, *ETR*, and *qL* of AM group reached their highest values on 14d. Compared with DN group, the parameters of *Fv/Fm*, *ΦPSII*, *qP*, *qL*, *ETR*, *NPQ*, etc. in *P. ternata* in DA group all increased to varying degrees, and most of the increases reached a significant level. After 14 days of natural drought, *ΦPSII*, and *ETR* significantly increased by 22.64% (Tab. 3).

Effect of AMF treatments on REL and osmotic substances

Under conditions of adequate watering, the introduction of AMF led to a decrease in Pro content while stabilized REL in leaves. Conversely, drought conditions caused a significant rise in both Pro

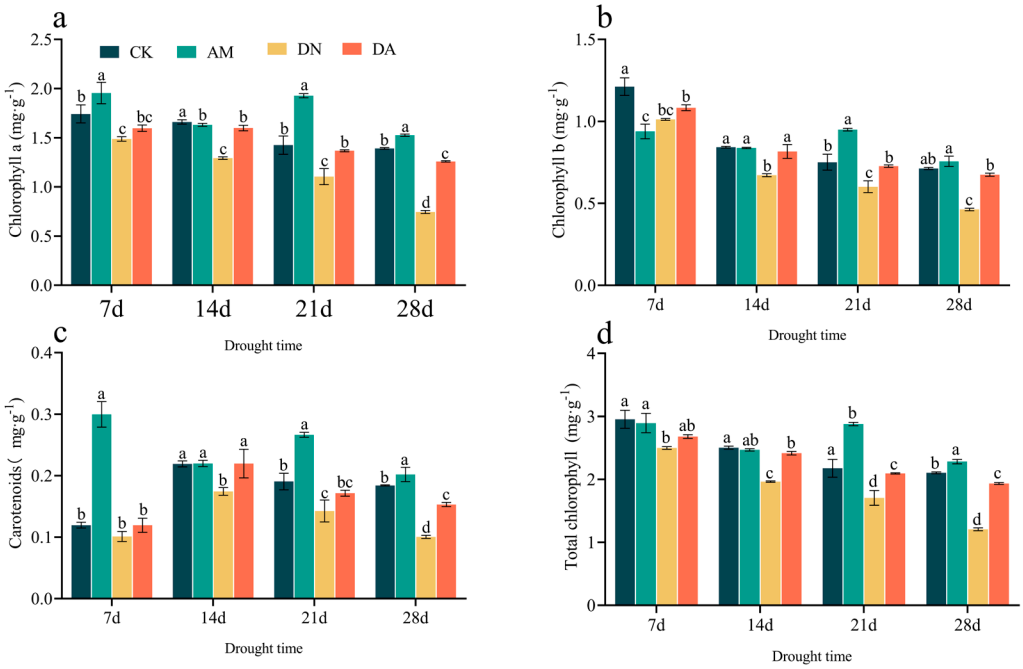

Fig. 4: Effects of AMF treatments on chlorophyll-a, chlorophyll-b, Car, and total chlorophyll of *P. ternata* at different experimental stages. Different letters above the error bars (n=3), $P<0.05$. AMF: arbuscular mycorrhizal fungus.

Tab. 2: Effects of AMF treatments. on *Pn*, *Gs*, *Ci*, *Tr*, and *WUE* of *P. ternata* at different experimental stages.

time	Group	Pn (mol·m-2·s^{-1})	Ci (mol·mol^{-1})	Gs (mol·m-2·s^{-1})	Tr (μmol·m-2·s^{-1})	WUE (mmol·mol^{-1})
7d	CK	7.667±0.208a	310.333±1.528b	142.667±2.517c	2.883±0.040b	2.659±0.057a
	AM	8.267±0.153a	378.667±0.577b	122.667±2.082a	3.103±0.040c	2.664±0.033b
	DN	7.200±0.361b	315.667±4.163c	133.333±2.309d	3.383±0.015d	2.128±0.102a
	DA	6.100±0.265b	344.000±4.000a	104.000±10.440b	3.180±0.061b	1.918±0.049b
14d	CK	8.467±0.462a	307.000±3.464a	188.667±1.528b	4.277±0.025b	1.980±0.119c
	AM	8.067±0.208a	327.333±15.885b	164.333±28.937a	3.817±0.449a	2.139±0.327d
	DN	8.100±0.200c	377.667±2.887b	199.333±4.163c	3.923±0.042c	2.065±0.068a
	DA	6.633±0.058b	354.667±3.215c	158.000±4.583c	3.533±0.067c	1.878±0.052b
21d	CK	6.467±0.635b	285.333±6.351b	98.000±3.464b	2.580±0.069b	2.503±0.176b
	AM	5.367±0.231a	313.333±5.508a	52.000±1.000a	1.323±0.031a	4.054±0.093b
	DN	3.967±0.115d	261.333±5.508d	43.667±1.155c	1.010±0.017d	3.929±0.159a
	DA	1.667±0.115c	267.000±8.185c	16.000±1.000c	0.570±0.035c	2.927±0.187a
28d	CK	6.367±0.289a	324.667±4.041a	149.667±0.577b	3.647±0.025b	1.746±0.091b
	AM	6.167±0.153a	265.000±1.000a	62.000±2.000a	1.850±0.050a	3.333±0.018b
	DN	4.833±0.351b	283.333±14.503b	46.333±0.577c	1.113±0.006d	4.340±0.295a
	DA	2.100±0.608b	254.667±20.648b	23.333±0.577c	0.790±0.010c	3.336±0.444a

Different letters above the error bars (n=3), $P<0.05$.

content and REL in leaves, indicating severe stress in seedlings. The pretreatment with AMF notably mitigated the rise in Pro content and REL values compared to CK. Drought exerted minimal influence on SS levels in *P. ternata*. Following 14 days of natural drought, soluble protein levels were markedly higher than those in the CK group. AMF inoculation considerably enhanced both soluble protein and SS content, with peaked levels on 21d in the DA group (Fig. 5).

Effect of AMF treatments on antioxidant enzyme activities

Under drought stress, the antioxidant enzyme activity of *P. ternata* leaves significantly increased after inoculation with AMF ($P<0.05$). Under well-watering conditions, inoculation of AMF increased the antioxidant enzyme activity to varying degrees. On 14d, POD activity (63.80%) on 14d, GSH content (32.67%) on 21d, and CAT activity (36.46%) on 28d were significantly higher than the CK group. The GSH content reached its highest after 7 days of natural drought. On the 28th day, the highest CAT activity was observed in AM group, significantly higher by 46.69% compared with the non-inoculation group. After 21 days of natural drought, POD activity in the DA group was the highest, significantly higher by 117.80% compared with the non-inoculation group (Fig. 6).

Correlation analysis of various indicators under different treatments

Through correlation analysis of photosynthetic and physiological indicators under different treatments (Fig. 7), chlorophyll-a, chloro-

Tab. 3: Effects of AMF treatments on the energy of *Fv/Fm*, *Fv'/Fm'*, *ΦPSII*, *ETR*, *qP*, *qL*, and *NPQ* of *P. ternata* at different experimental stages.

Time	Group	Fv/Fm	Fv'/Fm'	ΦPSII	ETR	qP	qL	NPQ
7d	CK	0.705±0.004a	0.391±0.009a	0.072±0.004b	36.308±2.018b	0.185±0.013b	0.121±0.010ab	1.456±0.130a
	AM	0.691±0.016a	0.410±0.009a	0.078±0.006a	39.144±3.201a	0.189±0.018a	0.121±0.014a	1.115±0.039a
	DN	0.709±0.009a	0.440±0.011a	0.082±0.007ab	41.328±3.528ab	0.187±0.019b	0.114±0.014b	1.294±0.078a
	DA	0.661±0.034a	0.391±0.021a	0.062±0.005ab	31.257±2.672ab	0.159±0.008ab	0.103±0.004ab	1.074±0.106a
14d	CK	0.693±0.014ab	0.406±0.019a	0.086±0.005ab	43.176±2.486ab	0.211±0.006ab	0.137±0.006ab	1.287±0.082b
	AM	0.717±0.014a	0.400±0.024ab	0.091±0.016a	45.902±8.304a	0.228±0.037a	0.151±0.027a	1.608±0.103a
	DN	0.709±0.020b	0.422±0.007b	0.078±0.003c	39.144±1.615c	0.184±0.011b	0.115±0.009b	1.184±0.130bc
	DA	0.689±0.010ab	0.403±0.011ab	0.065±0.004bc	32.760±1.817bc	0.162±0.009b	0.103±0.007ab	1.211±0.080b
21d	CK	0.690±0.006a	0.419±0.005a	0.079±0.001a	39.648±0.291a	0.188±0.004a	0.119±0.004a	1.299±0.211a
	AM	0.658±0.014a	0.365±0.003ab	0.053±0.002a	26.712±0.998a	0.145±0.004a	0.097±0.003a	1.145±0.016ab
	DN	0.633±0.017b	0.362±0.003c	0.039±0.003b	19.667±1.341b	0.109±0.007b	0.072±0.005b	1.021±0.039b
	DA	0.591±0.007b	0.393±0.006b	0.025±0.003b	12.573±1.379b	0.063±0.006b	0.039±0.004b	0.877±0.045a
28d	CK	0.706±0.010ab	0.402±0.004a	0.079±0.004a	39.648±1.770a	0.196±0.007a	0.126±0.005a	1.437±0.064ab
	AM	0.676±0.024a	0.390±0.011a	0.065±0.005a	32.760±2.310a	0.167±0.017a	0.109±0.013a	1.283±0.018a
	DN	0.670±0.006c	0.407±0.017a	0.049±0.005c	24.710±2.320c	0.120±0.008b	0.075±0.004c	1.250±0.060b
	DA	0.612±0.010bc	0.404±0.003a	0.036±0.003b	17.976±1.262b	0.088±0.006c	0.054±0.004b	1.052±0.080ab

Different letters above the error bars(n=3), $P < 0.05$.

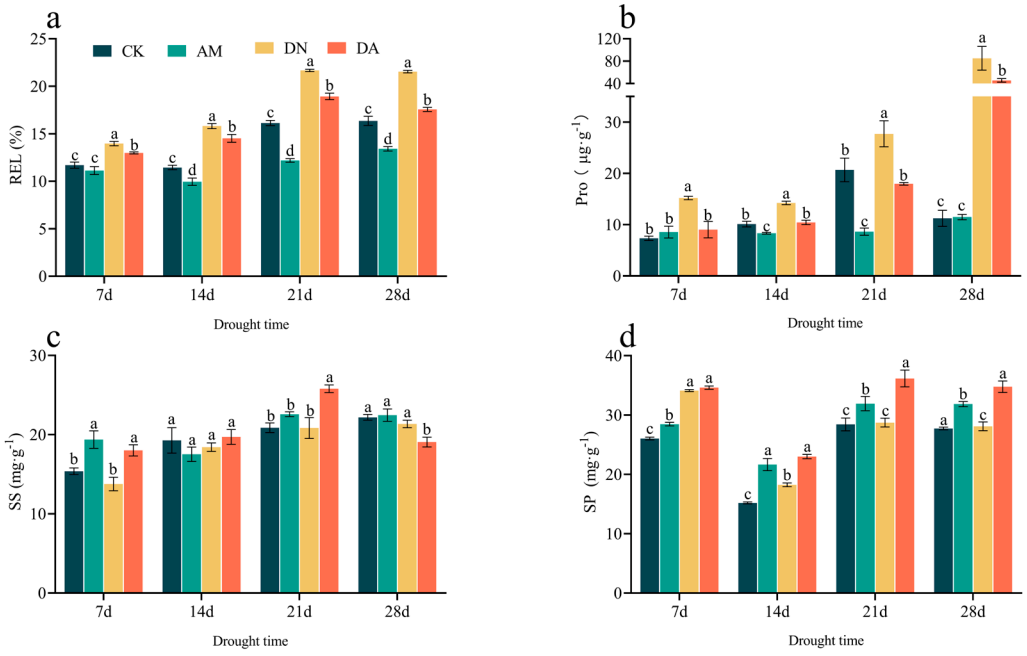

Fig. 5: Effects of AMF treatments on Pro, REL, SS, and SP of *P. ternata* at different experimental stages. Different letters above the error bars (n=3), $P< 0.05$.

phyll-b, Car, and total chlorophyll were significantly positively correlated with most gas exchange parameters and chlorophyll fluorescence parameters, GSH, and CAT. While significantly negative associations were found with *WUE*, Pro, and electrical conductivity. CAT was significantly negatively correlated with RLE and Pro, positively correlated with SOD and POD, and negatively correlated with SS and SP.

OPLS-DA of physiological indicators

Through OPLS-DA, R2X was 0 874, R2Y was 0.934, and Q2 was 0.882, all of which were close to 1, indicating the stability and reliability of this model, with good fitting and predictive ability. Using VIP>1 as the screening criterion, the VIP values of *WUE*, Car, *Gs*, *Tr*, REL, Pro, *Pn*, chlorophyll-a, *ETR*, *ΦPSII*, *qP*, and *qL* were 1.612, 1.610, 1.568, 1.535, 1.499, 1.314, 1.239, 1.162, 1.109, 1.109, 1.044, and 1.016, respectively, indicating significant importance of these indicators in drought treatment. As shown in Fig. 11, AM group and CK group can separate slightly on the PC1 axis, and the DN group and DA group had slight overlapping (Fig. 8).

Multivariate analyses revealed that drought stress, AMF inoculation, time, and their interactions all had significant effects on chlorophyll-a, chlorophyll-b, Car, total chlorophyll, *Gs*, Pro, POD, and CAT (all $P<0.01$). The interaction between time, AMF inoculation, and drought stress had significant effects on chlorophyll-a, chlorophyll-b, Car, total chlorophyll, Pro, REL, SP, POD, SS, *Pn*, Ci, *Fv'/Fm'*, *ΦPSII*, *ETR*, *NPQ*, and CAT (all $P<0.05$). Collectively, AMF inoculation may exert positive effect on the growth of *P. ternata* under interacted conditions (Tab. 4).

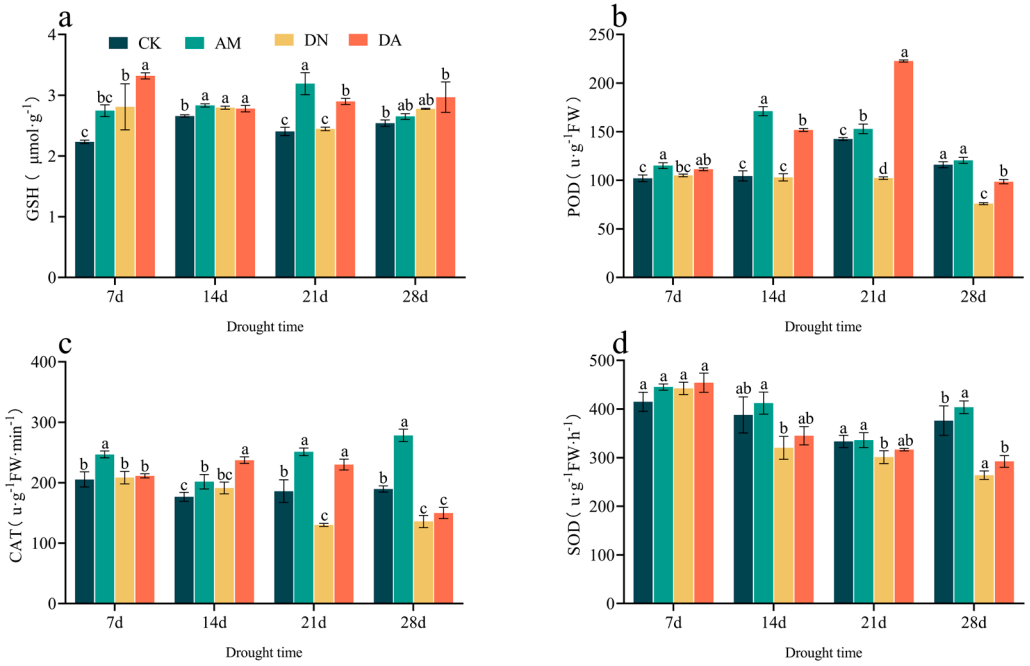

Fig. 6: Effects of AMF treatments on CAT, GSH, POD, and SOD of *P. ternata* at different experimental stages. Different letters above the error bars, $P < 0.05$.

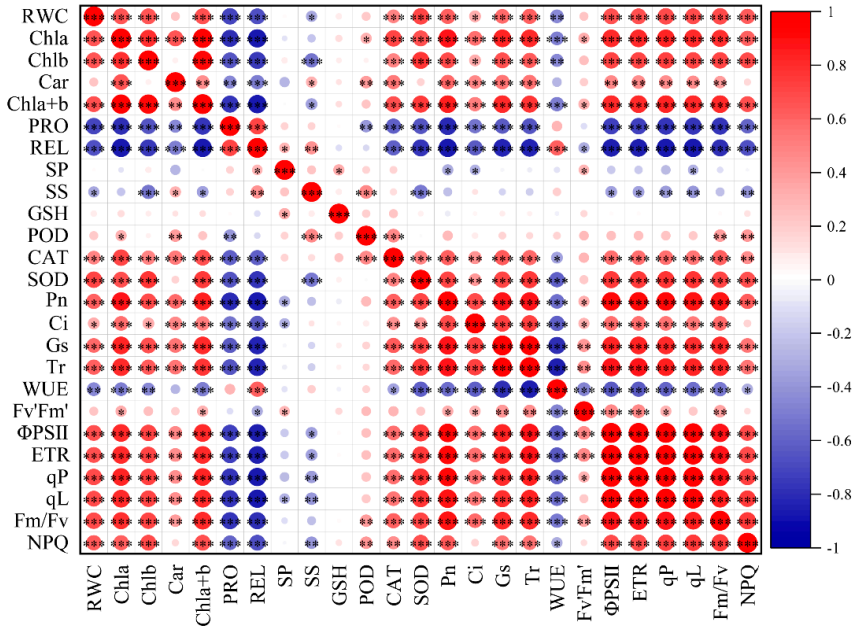

Fig. 7: Research on the correlation between physiological and photosynthetic indicators of *P. ternata* under different treatments.

Effect of AMF treatments on expression of AQPs

The expression of AQPs, including *Pt*NIP-1, NIP-2, PIP-1, PIP-2, PIP-3, TIP-2, TIP-3, TIP-5 and TIP-6, were detected to be varied under different treatments. Following AMF inoculation, an increase in the expression of AQPs was noted in all instances. On 7d, the highest relative expression levels were recorded for NIP-2, PIP-2, PIP-3, and TIP-5. During the period from 14d to 21d, there were significantly low relative expression levels for NIP-2, TIP-2, TIP-5, and TIP-6 in the DN group. After 7 and 14 days of drought stress, there was an upregulation trend in NIP-1 and TIP-3 genes, while downregulation in NIP-2, PIP-2, PIP-3, TIP-2, TIP-5, and TIP-6. A notable upregulation was evident in the DA group compared to the DN group (Fig. 9).

Discussion

Medicinal plants at different growth phases may frequently react to external drought conditions through a range of intricate physiological and biochemical processes (Li et al., 2022). Drought stress leads to numerous harmful impacts on plants, which include osmotic imbalance, damage to membrane systems, disturbances in cellular metabolism, and irregularities in water distribution (Guo et al., 2020). After inoculation with AMF, the resistance of many plants to drought stress can be strengthened, such as corn (Begum et al., 2019), tomatoes (Zhang et al., 2024), citrus (Wu et al., 2013), grapes (Ye et al., 2023), etc. The network of external hyphae formed by mycorrhizae is crucial to enhance nutrient absorption and water uptake (Han et al.,

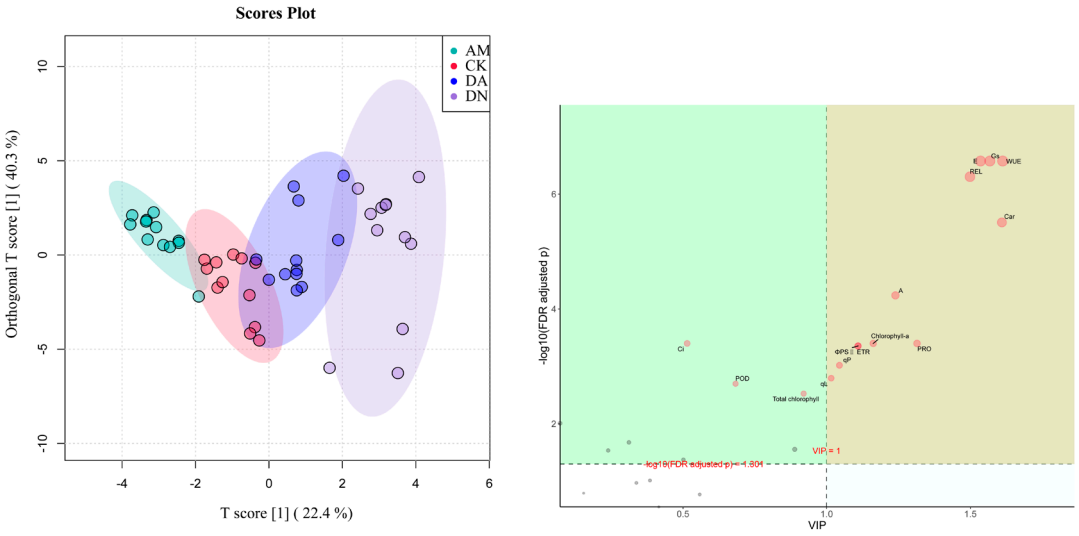

Fig. 8: OPLS-DA results of physiological indices of *P. ternata* under different drought and inoculation conditions

Tab. 4: Effects of AMF inoculation, drought time and degree and their interactions on physiological and biochemical parameters of *P. ternata*

Dependent variables	Independent variables						
	Time	AMF	Drought	AMF×Drought	Time×AMF	Time×Drought	Time×AMF ×Drought
RWC	7.087***	7.909**	8.836**	2.249ns	1.775ns	5.216**	0.44ns
Chla	182.714***	306.347***	593.566***	10.56**	17.562***	17.678***	29.295***
Chlb	487.448***	67.728***	226.493***	86.768***	54.656***	20.778***	29.225***
Car	57.489***	268.122***	410.695***	25.457***	27.279***	24.677***	55.639***
Total chlorophyll	299.851***	230.384***	505.691***	33.225***	28.305***	18.425***	22.029***
Pn	231.189***	29.578***	1009.796***	0.002ns	2.033ns	42.992***	4.414**
Ci	8.735***	0.916ns	557.968***	0.79ns	63.808***	58.65***	13.614***
Gs	154.737***	228.744***	1528.194***	54.223***	4.606**	58.928***	10.162***
Tr	270.406***	320.983***	3074.539***	15.584***	40.514***	222.136***	1.002ns
WUE	65.918***	21.505***	426.264***	2.35ns	21.633***	77.722***	2.724ns
Fv/Fm	4.474**	4.978*	18.855***	5.415**	0.982ns	14.775***	8.945***
ΦPSII	68.686***	19.225***	201.814***	0.277ns	1.482ns	23.904***	3.318*
ETR	68.635***	19.234***	201.677***	0.28ns	1.491ns	23.83***	3.313*
qP	75.2***	17.133***	179.561***	-	1.823ns	18.374***	1.704ns
qL	64.616***	13.068***	136.196***	0.234ns	1.855ns	12.473***	1.409ns
Fv‘/Fm‘	35.014***	14.059***	90.977***	1.908ns	1.309ns	12.244***	1.693ns
NPQ	25.65***	22.952***	16.163***	2.312ns	7.047***	1.998ns	8.878***
Pro	70.704***	32.5***	122.418***	13.905***	6.68***	61.061***	9.243***
REL	971.046***	706.785***	2640.064***	0.005ns	65.139***	100.341***	8.085***
SP	740.588***	458.025***	249.79***	2.975ns	23.17***	37.158***	12.608***
SS	120.629***	42.039***	1.964ns	4.392**	28.319***	13.459***	8.158***
GSH	0.338ns	82.114***	26.254***	2.201ns	12.464***	16.41***	1.552ns
POD	778.564***	1806.269***	61.581***	226.422***	284.67***	124.371***	284.066***
CAT	20.091***	309.168***	122.537***	6.828**	22.758***	79.143***	22.068***
SOD	94.53***	14.449***	74.384***	0.011ns	0.578ns	26.448***	0.359ns

ns P<0.05; * P<0.05; ** P<0.01; and ***P<0.001

2022). AMF are capable of modulating physiological and molecular mechanisms, allowing the host plants to withstand drought stress, while also exhibiting a robust capacity to mitigate drought-induced oxidative damage through improved antioxidant defenses (ZOU et al., 2021). This research demonstrated the beneficial effects of AMF on the growth of *P. ternata*.

Soil water scarcity significantly affects plant growth and increases the production of reactive oxygen species (ROS), which damage plants by oxidizing photosynthetic pigments, proteins, membrane lipids, and nucleic acids (JAN et al., 2022). Inoculation with AMF in our study increased CAT, POD, and SOD activities under different degrees of drought. Similarly, ZHANG et al. (2014) found that AMF-inoculated *Cyclobalanopsis glauca* seedlings had greater SOD and POD activities under drought conditions. Under adverse environmental conditions, plants can survive by maintaining ROS formation-detoxification equilibrium through the activation of the enzymatic-nonenzymatic antioxidant-comprised anti-oxidant defense system to mitigate oxidative damage (HOSSAIN et al., 2020).

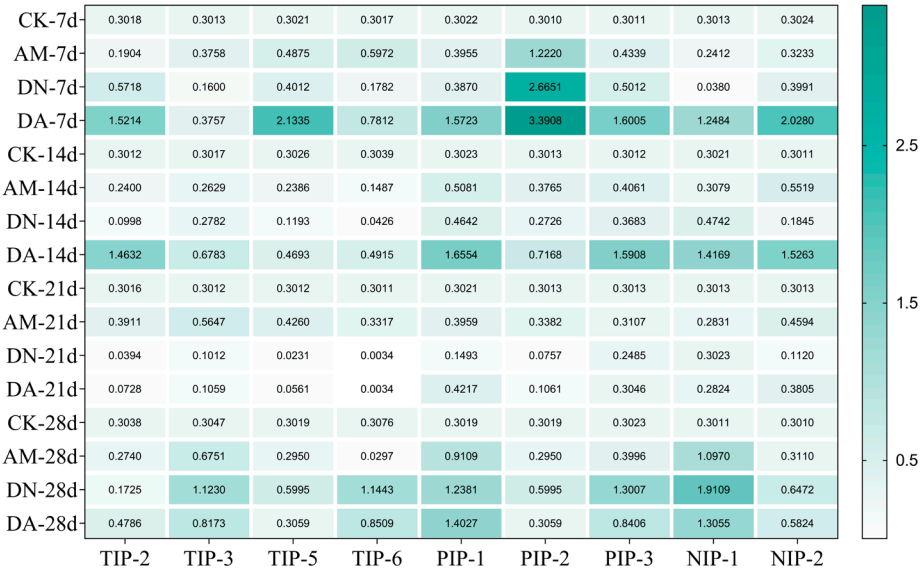

Fig. 9: Relative expression of AQPs in leaves of *P. ternata* under different treatments.

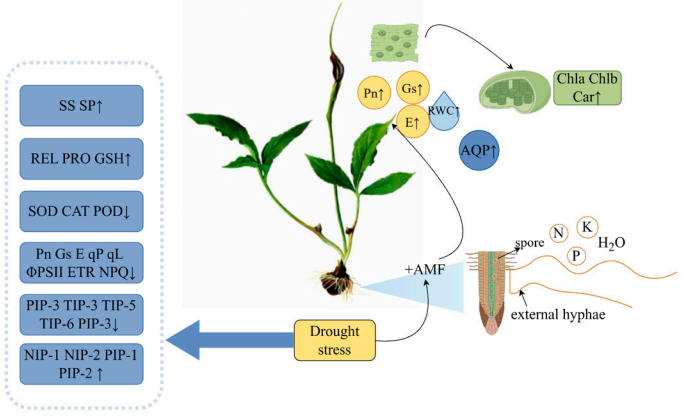

Fig. 10: Mechanism diagram of AMF in alleviating drought stress.

The process of photosynthesis is a physicochemical mechanism that converts light energy into chemical energy, supplying the essential organic components required for plants during their growth and development stages (YANG et al., 2014). AMF obtain photosynthetic carbohydrates and carbon from roots of host plants, while facilitating soil-to-plant delivery of nutrients and water via their extensive hyphal networks (MATHUR et al., 2018). *P. ternata* inoculated with AMF had higher *Gs*, *Tr* and net *Pn*, and lower intercellular CO2 concentrations than those of *P. ternata* without AMF inoculation under drought stress. It can be attributed to more water uptake by the extraradical hyphae in mycorrhizal roots. It may consequently improve the water content and enhance *Pn* by either improving root hydraulic conductivity or modifying root structure (JAJOO and MATHUR, 2021). Collectively, colonization by AMF may boost photosynthesis by enhancing the gas exchange ability of *P. ternata* under drought stress. Similarly, Abeer Hashem et al. also demonstrated that inoculation with AMF under drought stress can significantly increase the chlorophyll content and improve the *Pn* of chickpeas (HASHEM et al., 2019). This study found decreased content of chlorophyll and Car in *P. ternata* under drought stress. While AMF inoculation under drought stress reversed and increased the content of chlorophyll and Car significantly. AMF was also found to significantly increase chlorophyll content and increase *Pn*, *Gs*, *Tr*, and carbohydrate accumulation of wheat under cadmium stress (LI et al., 2023). In this study, under drought stress, the soluble sugar and soluble protein content in the leaves of Pinellia ternata inoculated with AMF were higher than those in the non inoculated group, while the electrical conductivity was lower than that in the non inoculated group, thus maintaining a cellular balance to resist drought stress. The symbiotic combination with AMF promotes drought resistance by increasing the rate of photosynthesis, leading to the accumulation of carbohydrates as osmoprotectants (AKHOUNDNEJAD and BARAN, 2023).

AMF symbiosis can indirectly enhance the improvement of water conditions Gas exchange capacity and photochemical and non photochemical efficiency PSII (YE et al., 2023). We found through correlation analysis that RWC is significantly positively correlated with chlorophyll fluorescence parameters. Studies have shown that inoculation with AMF improves photosynthesis and PSII function absorption under drought conditions by improving water content, stabilizing chloroplast and membrane structures, increasing Rubisco content, and reducing the accumulation of free radicals (MO et al., 2016).

AQPs can participate in physiological processes such as seed germination, stomatal movement, photosynthesis, and cell elongation (UEHLEIN et al., 2007). Through inoculation with AMF in our experiment, diverse effects on AQPs expression of *P. ternata* were observed under well-watering. It included up-regulated PtNIP-2, PtPIP-1, PtPIP-3, PtTIP-2, PtTIP-3, and PtTIP-5; down-regulated PtTIP-6; as well as non-respondent PtNIP-1 and PtPIP-2, showing more up-regulated AQPs than the down-regulated gene. It supported that mycorrhization could induce the expression of more AQPs, which could improve water content of host plants by accelerating water absorption. LIU et al (2016) found that inoculation with *R. irregularis* down-regulated the expression of PIP2; 1, PIP2; 2 while up-regulating the expression of PIP1; 1, PIP1; 3, PIP1; 4, PIP1; 5, PIP2; 1, PIP2; 2, and PIP2; 3 in leaf of *Populus×canadensis 'Neva'* under drought stress. It could suggest improved water transport according to up-regulation of host AQPs under AMF inoculation; and reduced water loss as indicated by the down-regulated host AQPs under mycorrhization.

Conclusion

AMF inoculation demonstrates positive effects on enhancing the growth of *P. ternata* under drought stress, which can improve antioxidant enzyme activity, chlorophyll content, osmotic regulating substance, photosynthetic capacity, while reducing REL and up-regulating AQP expression. AMF can be utilized as beneficial fungi

to enhance drought tolerance in *P. ternata*. However, the specific molecular mechanism underlying the mycorrhizal enhancement of drought tolerance in drought-stressed *P. ternata* remains unknown and warrants further investigation.

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Conflict of interest
No potential conflict of interest was reported by the authors.

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