Differential Responses of Atriplex canescens and Tamarix ramosissima to Soil Drought: Postprint

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Abstract

In the construction of shelter forests in arid regions, the selection of plant species with robust stress resistance and adaptability is paramount. Through potted water control experiments simulating varying drought gradients, we compared the differential ecological adaptability to drought stress between *Atriplex canescens*, an introduced species in the Tarim Basin, and *Tamarix ramosissima*, a native species. The results demonstrated: (1) With escalating drought severity, leaf water content in both *Atriplex canescens* and *Tamarix ramosissima* progressively declined, whereas water retention capacity, proline content, and relative electrical conductivity progressively increased. The soluble sugar content in *Atriplex canescens* and the malondialdehyde content in *Tamarix ramosissima* attained maximal values under mild and severe drought conditions, respectively, with *Tamarix ramosissima* exhibiting more pronounced increments. (2) POD activity in both species gradually increased; under severe drought, the percentage increase relative to the control in *Tamarix ramosissima* was approximately threefold that of *Atriplex canescens*; under moderate drought, SOD activity peaked, with the percentage increase relative to the control in *Tamarix ramosissima* being approximately fivefold that of *Atriplex canescens*. The magnitude of change in both enzyme activities was greater in *Tamarix ramosissima* than in *Atriplex canescens*. (3) Chlorophyll content in both species followed the sequence: mild drought > control > moderate drought > severe drought. The net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration in *Tamarix ramosissima* all decreased progressively, whereas mild drought exerted a slight promotional effect on chlorophyll content and photosynthetic capacity in *Atriplex canescens*. (4) Correlation and principal component analyses revealed that under drought stress, the interconnections among traits were more tightly coupled in *Tamarix ramosissima*, while *Atriplex canescens* exhibited relative conservatism, being less prone to altering traits and their relationships. *Atriplex canescens* experienced less impact from drought stress, with marginally superior drought adaptability compared

to *Tamarix ramosissima*.

Full Text

Differences in the Response to Soil Drought Between Atriplex canescens and Tamarix ramosissima

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Abstract

Selecting plant species with strong stress resistance and adaptability is crucial for shelter forest construction in arid regions. This study compared the ecological adaptability to drought stress between the introduced species *Atriplex canescens* and the native species *Tamarix ramosissima* in the Tarim Basin through a pot water control experiment simulating different drought gradients. The results showed that: (1) As drought severity increased, leaf water content in both species gradually decreased, while water retention capacity, proline content, and relative conductivity gradually increased. The soluble sugar content of *A. canescens* and the malondialdehyde content of *T. ramosissima* reached maximum values under mild and severe drought, respectively, with greater increases observed in *T. ramosissima*. (2) Peroxidase (POD) activity in both species gradually increased; under severe drought, the percentage increase in *T. ramosissima* was approximately three times that of *A. canescens*. Superoxide dismutase (SOD) activity peaked under moderate drought, with the percentage increase in *T. ramosissima* being approximately five times that of *A. canescens*. The changes in both enzyme activities were greater in *T. ramosissima* than in *A. canescens*. (3) The chlorophyll content in both species followed the pattern: mild drought > control > moderate drought > severe drought. The net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration of *T. ramosissima* gradually decreased, while mild drought slightly promoted chlorophyll synthesis and photosynthetic capacity in *A. canescens*. (4) Correlation and principal component analysis revealed that the relationships among traits in *T. ramosissima* were more tightly linked under drought stress, whereas *A. canescens* was relatively conservative and less prone to altering trait relationships. Overall, *A. canescens* was less affected by drought stress and exhibited slightly stronger drought adaptability than *T. ramosissima*.

Keywords: *Atriplex canescens*; *Tamarix ramosissima*; physiological characteristics; drought adaptability

Introduction

Northwest China is a typical ecologically fragile region with sparse vegetation, harsh environmental conditions, frequent wind-sand events, and severe soil erosion. Planting drought-resistant species with stable growth represents the most economical and effective measure for soil and water conservation and windbreak sand fixation. Understanding plant adaptability to stress is essential for screening and selecting species with strong adaptability to achieve these goals. Drought stress is a common abiotic stress factor, and plant survival and growth under drought conditions depend not only on structural characteristics but also on tolerance and adaptability to the environment. Severe drought stress weakens photosynthesis, induces stomatal closure, inhibits plant growth, and triggers a series of stress responses. Under drought stress, plant cells generate reactive oxygen species (ROS), and high ROS levels damage cell membrane structures and affect cellular metabolism. Plants possess efficient enzymatic antioxidants (such as superoxide dismutase, peroxidase, catalase, and glutathione reductase) and non-enzymatic antioxidants (such as carotenoids and glutathione) to scavenge excess ROS. Additionally, drought stress induces lipid peroxidation, producing malondialdehyde (MDA) that damages membrane systems. A series of osmotic adjustment substances (such as proline, soluble sugars, and soluble proteins) increase in content to regulate osmotic balance and adapt to arid environments. Therefore, under drought stress, plants adapt through reduced transpiration, stomatal closure, improved water use efficiency, accumulation of osmotic adjustment substances, and enhanced enzyme activity, with these changes directly reflecting plant adaptability to drought.

Atriplex canescens, a species of the genus *Atriplex* in the Amaranthaceae family, is widely distributed in arid and semi-arid regions. It can be used for windbreak sand fixation, saline-alkali land improvement, and heavy metal pollution remediation, making it an excellent shrub for ecological restoration and soil and water conservation. Its leaves are rich in crude protein and various nutrients, serving as a high-quality forage resource. *A. canescens* has been introduced to the Tarim Basin and widely planted, showing good growth in wind-sand front zones. *Tamarix ramosissima* is distributed along riverbanks and among sand dunes in the Tarim Basin, with strong tolerance to high temperature, cold, salinity, and extreme drought, playing an important role in the desert ecosystem. Both species exhibit strong adaptability and high economic value, making them suitable for natural conditions in wind-sand front zones and promising materials for vegetation restoration and agricultural development in northwestern arid desert regions. However, the adaptive characteristics of the introduced species *A. canescens* to local conditions and its differences from the native species *T.*

ramosissima remain unclear.

This study comprehensively analyzed the responses of water physiology, photosynthesis, osmotic adjustment, and oxidative defense in *T. ramosissima* and *A. canescens* under drought stress to compare their adaptability differences to soil drought, providing theoretical support for shelter forest construction and forage resource development in arid regions.

Materials and Methods

1.1 Experimental Site Overview

The experiment was conducted at the Horticulture and Forestry College of Tarim University in Aral City, Southern Xinjiang (81°27 E, 40°54 N). The region has a warm temperate continental arid desert climate with an extreme minimum temperature of -28°C, annual solar radiation of 133.7–146.3 Kcal $\cdot$ cm^{-2}, annual sunshine hours of 2,991.8 h, and scarce rainfall with an average annual precipitation of 1876.6–2558.9 mm. The monthly average minimum temperature ranges from 0.31 to 0.12 $g \cdot kg^{-1}$, and the soil is predominantly desert sandy soil.

1.2.1 Experimental Materials

Atriplex canescens seeds were soaked in warm water at 40°C for 24 hours for germination. When half of the seeds showed radicle emergence, they were sown in soil and managed to ensure normal seedling growth. *Tamarix ramosissima* seedlings were collected from the riverbank of Regiment 11 in Aral City (81°71 E, 40°47 N).

1.2.2 Treatment Methods

In May, uniform seedlings were transplanted into pots (one plant per pot), with 40 pots per species. The potting soil was desert riparian sandy soil (1.51 $g \cdot cm^{-3}$ bulk density, 24.2% total nitrogen, 11.91 $g \cdot kg^{-1}$ total phosphorus, 16.14 $g \cdot kg^{-1}$ total carbon, 0.12 $g \cdot kg^{-1}$ field capacity measured by the ring knife method). After transplanting, all pots received identical appropriate water and fertilizer management.

In early July, based on the Chinese agricultural soil drought classification standard (GB/T 32136-2015), four moisture gradients were established: 70–80% of field capacity as control (no water stress), 50–60% as mild drought, 30–40% as moderate drought, and 10–20% as severe drought. Before treatment, all pots were fully watered. Soil water content was measured daily until reaching the target gradient, after which it was maintained by daily weighing and watering. The treatment lasted for 60 days.

1.2.3 Index Measurement and Methods

Photosynthetic parameters were measured using a LI-6400XT portable photosynthesis system with a red-blue light source. Light intensity was set at 1500 mol·m^{-2}·s^{-1}, temperature at 25°C, and air flow rate at 500 mol·s^{-1}. A buffer bottle controlled the CO_2 concentration in the reference chamber to match the external environment. On clear days from 10:00–11:00, net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), and intercellular CO_2 concentration (Ci) were measured on mature, healthy leaves from the same direction and height. Leaves smaller than the leaf chamber area were scanned with a scanner, and actual leaf area was calculated using ImageJ software before re-entering the photosynthesis system for calculation. Concurrently, pest-free mature leaves (third to fifth leaf from the top) were placed in labeled ziplock bags, transported to the laboratory in an ice box, and used for measurements. Five fresh leaves were selected to determine relative water content (RWC) and water retention capacity, while remaining leaves were snap-frozen in liquid nitrogen and stored at -80°C for physiological and biochemical assays.

Water use efficiency (WUE) was calculated as WUE = Pn/Tr. Peroxidase (POD) activity and superoxide dismutase (SOD) activity were measured using the guaiacol method and nitroblue tetrazolium colorimetric method, respectively. Relative conductivity was determined using a conductivity meter. Chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid contents were extracted using the ethanol immersion method. Soluble sugar content was measured by the anthrone colorimetric method, proline content by acidic ninhydrin colorimetry, and malondialdehyde (MDA) content by the thiobarbituric acid method. Leaf relative water content was determined by the immersion-drying method, and water retention capacity by the detached hanging air-drying method (24 h).

1.2.4 Data Analysis

Experimental data were analyzed using SPSS 26.0 software, with Duncan' s method for multiple comparisons ($\alpha = 0.05$). Data were organized using Microsoft Excel 2019, and figures were created using Origin 2022. All data in figures and tables are presented as mean ± standard deviation.

Results and Analysis

2.1 Effects of Soil Drought Stress on Leaf Relative Water Content and Water Retention Capacity

As soil drought severity increased, the relative water content of leaves in both shrub species continued to decrease. Under mild, moderate, and severe drought treatments, the relative water content of *A. canescens* leaves decreased by 6.15%, 7.60%, and 9.67% compared with the control, respectively, while that of *T. ramosissima* leaves decreased by 2.59%, 5.46%, and 14.41%, respectively, showing a greater reduction in *A. canescens*. Conversely, water retention capacity increased with drought severity. Compared with the control, water retention capacity in *A. canescens* leaves increased by 21.14%, 45.67%, and 68.06% under mild, moderate, and severe drought, respectively, while *T. ramosissima* leaves showed increases of 32.70%, 51.81%, and 52.94%, respectively, with greater increases in *T. ramosissima*.

2.2 Effects of Soil Drought on Leaf Relative Conductivity and Enzyme Activity

As soil drought severity increased, the relative conductivity of leaves in both shrub species showed an increasing trend, with significant differences from the control. Soil drought treatments increased relative conductivity in *A. canescens* leaves, but no significant differences were observed among drought treatments ($P > 0.05$). The relative conductivity of *T. ramosissima* leaves under severe drought was significantly higher than under other treatments, increasing by 41.31% compared with the control. Malondialdehyde content in *T. ramosissima* reached its maximum under severe drought, increasing by 154.99% compared with the control, while *A. canescens* MDA content peaked under mild drought, increasing by 16.50% compared with the control.

Superoxide dismutase (SOD) activity in both species showed a trend of first increasing then decreasing with drought severity, while peroxidase (POD) activity gradually increased. Moderate soil drought promoted SOD activity, with *A. canescens* and *T. ramosissima* showing increases of 29.17% and 163.56% compared with the control, respectively, with more pronounced accumulation in *T. ramosissima*. Soil drought increased POD activity in both species; under mild, moderate, and severe drought, *A. canescens* showed increases of 2.65%, 37.35%, and 51.83% compared with the control, respectively, while *T. ramosissima* showed increases of 98.69%, 158.43%, and 84.55%, respectively, with greater increases in *T. ramosissima*.

Proline content in both species gradually increased with drought severity, showing significant differences from the control. Under mild drought, proline content in *A. canescens* reached its maximum, increasing by 42.32% compared with the control, while *T. ramosissima* reached its maximum under moderate drought, increasing by 72.04% compared with the control. Under severe drought, proline content in both species increased to the highest level, with increases of 76.70% in *A. canescens* and 74.42% in *T. ramosissima*, showing a greater increase in *T. ramosissima*.

2.3 Effects of Soil Drought on Photosynthetic Pigments

As soil drought severity increased, soluble sugar content in *T. ramosissima* leaves gradually increased, while *A. canescens* leaves showed a trend of first increasing then decreasing. Under mild drought conditions, chlorophyll a, chlorophyll b, and total chlorophyll contents in *A. canescens* leaves increased by 6.74%, 10.05%, and 7.48% compared with the control, respectively, while *T. ramosissima* leaves showed increases of 5.21%, 7.21%, and 5.75%, respectively, with significantly greater increases in *A. canescens*. Under moderate and severe drought conditions, chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid contents in *A. canescens* leaves showed no significant differences compared with the control, while *T. ramosissima* leaves showed significant decreases of 9.59%, 37.70%, 42.67%, and 45.15% compared with the control, respectively, with greater reductions in *T. ramosissima* than in *A. canescens*.

[Figure 1: see original paper]

[Figure 2: see original paper]

2.4 Effects of Soil Drought on Photosynthetic Parameters

As drought severity increased, the net photosynthetic rate, stomatal conductance, transpiration rate, and water use efficiency of both species showed declining trends, though the patterns differed between species. Mild drought significantly promoted increases in net photosynthetic rate, stomatal conductance, and transpiration rate in *A. canescens* but had no significant effect on water use efficiency. For net photosynthetic rate, *A. canescens* reached its maximum under mild drought, increasing by 8.20% compared with the control, while decreasing by 19.66% and 45.69% under moderate and severe drought, respectively. *T. ramosissima* showed decreases of 11.20% and 28.08% under moderate and severe drought, respectively, with more pronounced reductions than in *A. canescens*.

For stomatal conductance, *A. canescens* increased by 30.00% under mild drought compared with the control, while *T. ramosissima* decreased by 25.00%. Under moderate and severe drought, stomatal conductance in both species decreased, with greater reductions in *T. ramosissima*. Transpiration rates in both species were significantly reduced under moderate and severe drought, with *T. ramosissima* decreasing by 55.15% and 65.24% compared with the control, respectively, while *A. canescens* decreased by 19.66% and 45.69%, respectively, showing greater reduction amplitude in *T. ramosissima*. Water use efficiency in *A. canescens* decreased by 11.20% under moderate drought and 28.08% under severe drought, while *T. ramosissima* decreased by 11.20% and 28.08%, respectively, with more obvious reduction in *T. ramosissima*. No significant differences were observed between species under moderate and severe drought stress.

2.5 Correlation Analysis and Principal Component Analysis

In *A. canescens*, leaf water content and pigment content showed significant positive correlations with photosynthetic parameters, while water retention capacity, proline content, and MDA content showed significant negative correlations with photosynthetic parameters. In *T. ramosissima*, all traits except SOD activity and soluble sugar content showed significant differences among each other, with water retention capacity, relative conductivity, MDA content, POD activity, proline content, and soluble sugar content showing significant negative correlations with photosynthetic parameters, while relative water content and photosynthetic pigment content showed significant positive correlations with photosynthetic parameters.

Principal component analysis was performed on 13 traits of both species, using a cumulative variance contribution rate greater than 85% as the criterion. The results showed that for *T. ramosissima*, the first three principal components accounted for 89.49% of the variance. The first principal component accounted for 52.08%, primarily comprising leaf water content, chlorophyll content, and photosynthetic parameters. The second principal component accounted for 23.69%, mainly composed of carotenoid and soluble sugar contents. The third principal component accounted for 14.03%, consisting of SOD activity, MDA content, and water use efficiency. The cumulative contribution rate of the first two principal components for *A. canescens* was 76.62%, with the first principal component accounting for 52.08% and primarily summarizing information for all indicators except SOD activity. The second principal component accounted for 24.54%, mainly composed of SOD activity, MDA content, and water use efficiency. The results differed significantly between species, with *T. ramosissima* showing tighter linkages among traits under drought stress.

[Figure 3: see original paper]

Discussion and Conclusion

Numerous studies have found that plants lose water under drought conditions, leading to reduced leaf water content. Simultaneously, plants prevent excessive dehydration and maintain normal growth and metabolism by enhancing cellular water retention capacity, increasing osmotic adjustment substance content, and reducing stomatal conductance. This study showed that as drought stress intensified, the relative water content of both *A. canescens* and *T. ramosissima* decreased linearly, while water retention capacity gradually increased. *A. canescens* showed a greater reduction in relative water content, while *T. ramosissima* showed a greater increase in water retention capacity under severe drought, likely due to long-term adaptation to arid environments resulting in increased leaf thickness and improved water storage capacity.

Under drought stress, plants accumulate reactive oxygen species and peroxides, causing membrane lipid peroxidation, reducing cell integrity, leading to electrolyte leakage and generating large amounts of the toxic end product MDA. In this study, MDA and relative conductivity contents under drought treatments were higher than in the control, but *T. ramosissima* showed a more pronounced response under severe drought, indicating higher degrees of membrane lipid peroxidation. Plants activate defense systems to counteract ROS toxicity under drought stress. Studies have shown that SOD activity in both *T. ramosissima* and *A. canescens* peaked at moderate drought levels, with *T. ramosissima* showing a 163.56% increase compared with the control, significantly greater than that in *A. canescens*. Under severe drought, both species showed maximum POD activity, with *T. ramosissima* increasing by 158.42% compared with the control, indicating more dramatic increases than in *A. ramosissima*. This suggests that *T. ramosissima* activated a stronger enzymatic defense mechanism.

Proline and soluble sugars serve as important osmotic adjustment substances that increase intracellular osmotic pressure and prevent cell dehydration. Proline, the most water-soluble amino acid, is non-toxic to plants, participates in chlorophyll synthesis, and acts as an effective organic osmotic regulator that helps tissues retain water and enhances drought resistance. Soluble sugars also function as important osmotic adjusters that reduce osmotic potential and enhance water absorption under water-limited conditions. This study found that soluble sugar and proline contents in both species were higher than in the control under all drought treatments, consistent with previous studies on *Tamarix*, *A. canescens*, and *Quercus fabri* under drought stress. *A. canescens* showed greater proline content increases, playing a key role in osmotic adjustment under drought stress.

Chlorophyll content plays a vital role in photosynthesis, and water deficit is an important factor in chlorophyll degradation. Studies have shown that chlorophyll and carotenoid contents peaked under mild drought stress, which was beneficial for photosynthetic pigment accumulation in both species. This is consistent with research on *A. canescens* and *Platycladus orientalis*, possibly because mild drought induces the plant protection system to increase chlorophyll content to maintain normal photosynthesis. As drought severity increased, the chlorophyll synthesis pathway suffered irreversible damage, leading to decreased chlorophyll content. Under mild drought, *A. canescens* showed increased pigment content and enhanced photosynthetic capacity, while *T. ramosissima* photosynthetic capacity continued to decline.

Factors inhibiting plant photosynthesis under drought conditions are multifaceted. Stomatal closure caused by drought is considered a determining factor, while stomatal conductance is controlled by interactions between the plant interior and external environment. Additionally, changes in photosynthetic enzyme activity, photosynthetic pigment composition, and imbalance in antioxidant defense may all affect photosynthesis under drought conditions. Correlation analysis indicated that the two species responded differently to drought environments, with *A. canescens* showing 23 pairs of significantly correlated traits and *T. ramosissima* showing 34 pairs. Principal component analysis revealed that *T. ramosissima* traits were more tightly linked under drought stress, while *A. canescens* was a relatively conservative species less prone to altering traits and trait relationships to adapt to drought. Previous studies have shown that species more susceptible to environmental stress are more likely to change traits and enhance compensatory and trade-off relationships among traits to adapt to drought environments, resulting in more diversified trait correlations. *T. ramosissima* showed tighter linkages among traits under drought stress, whereas *A.*

canescens was relatively conservative.

In conclusion, under drought conditions, *A. canescens* primarily copes with drought stress by increasing proline content, reducing plasma membrane permeability, decreasing MDA content, and maintaining relatively stable water use efficiency. *Tamarix ramosissima* mainly responds to drought by activating antioxidant enzyme mechanisms and enhancing leaf water retention capacity. *Atriplex canescens* is less affected by drought stress, less prone to trait changes, and exhibits stronger drought tolerance than *T. ramosissima*.

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Note: Figure translations are in progress. See original paper for figures.