Effects of Drought Stress on Growth and Physiology of Alhagi sparsifolia Seedlings (Postprint)

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Abstract

Leaves and roots can respond to drought stress through changes in morphology, physiology, and biomass accumulation. This study investigated the dominant species Alhagi sparsifolia Shap. in the Cele Oasis-Desert Ecotone. A pot experiment was conducted to simulate three water conditions (well-irrigated CK: soil water content at 70%~75% of maximum field capacity; mild stress W1: 50%~55% of field capacity; severe stress W2: 25%~30% of field capacity) to analyze variation characteristics of leaf and root growth and physiology in annual Alhagi sparsifolia seedlings, revealing adaptive strategies to drought stress. The results showed that: (1) Drought significantly inhibited growth of both aboveground and belowground organs in Alhagi sparsifolia, mainly manifested as significant reductions in leaf area, root length, root surface area, root tissue density, and soluble sugar content in leaves and roots ($P<0.05$), while leaf tissue density, leaf dry matter content, specific root length, and proline and malondialdehyde content in leaves and roots increased. (2) During the early growth stage, aboveground biomass accounted for a relatively large proportion across all treatments (root-to-shoot ratios were 0.43\$±0.14, 0.59±0.1, and0.83±0.83underCK, W1, andW2, respectively); whereasduringthelategrowthstage,
to − shootratiounderseverestress(3.12±\$0.32), indicating that Alhagi sparsifolia enhanced resource investment in belowground parts during the late growth stage, and this resource allocation pattern was more pronounced under severe drought stress. (3) Pearson correlation analysis indicated significant trade-off relationships between core traits related to leaf morphology and root physiology in Alhagi sparsifolia ($P<0.05$), while leaves and roots could undergo coordinated changes in physiological metabolism. These findings preliminarily demonstrate that Alhagi sparsifolia seedlings exhibit adaptive characteristics of high dry matter storage and defense capability with low water consumption under drought, can coordinate resource allocation between leaves and roots, and gradually form a strategy of slow investment and conservative growth

with increasing stress duration. These results provide a reference for desert vegetation restoration and management in this region.

Full Text

Effects of Drought Stress on Growth and Physiology of *Alhagi sparsifolia* Seedlings

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Abstract

Leaves and roots respond to drought stress through changes in morphology, physiology, and biomass accumulation. This study examined the dominant species *Alhagi sparsifolia* from the oasis-desert transition zone in Cele, analyzing growth and physiological changes in one-year-old seedlings via a pot experiment. Three water conditions were simulated: well-watered control (70%–75% field capacity, FC), mild stress (50%–55% FC), and severe stress (25%–30% FC). Results revealed: (1) Drought significantly inhibited growth of both above- and below-ground organs, manifested by significant decreases in leaf area, root length, root surface area, root tissue density, and soluble sugar content in leaves and roots ($P < 0.05$). Concurrently, leaf tissue density, leaf dry matter content, specific root length, and proline and malondialdehyde (MDA) contents in leaves and roots increased. (2) During early growth, aboveground biomass predominated across all treatments, with root-shoot ratios of 0.43 ± 0.14, 0.59 ± 0.10, and 0.83 ± 0.83 for control, mild, and severe stress, respectively. In late growth, belowground biomass predominated, with the highest root-shoot ratio (3.12 ± 0.32) under severe stress, indicating enhanced resource investment underground during late growth, particularly under severe drought. (3) Pearson correlation analysis demonstrated significant trade-offs between core traits linking leaf morphology and root physiology ($P < 0.05$), while physiological metabolism showed coordinated changes between leaves and roots. These findings suggest that *A. sparsifolia* seedlings exhibit adaptive characteristics of high dry matter storage and defense capacity with low water consumption, coordinating resource allocation between leaves and roots to form a slow-investment, conservative growth strategy as stress duration increases. These results provide a reference for desert vegetation restoration and management in this region.

Keywords: *Alhagi sparsifolia*; drought stress; morphological traits; biomass; leaf and root; adaptive strategy

Introduction

Drought is a critical environmental stressor that limits plant growth and development and affects ecosystem functions. It influences not only biomass accumulation and allocation among plant organs but also regulates morphological and physiological traits, subsequently affecting population structure and ecosystem function. Desert plants have evolved strong plasticity and ecological adaptability to drought stress through long-term evolution. Leaves and roots are sensitive organs that rapidly perceive drought stress, and their functional trait changes serve as a crucial link reflecting plant survival responses to environmental changes. Plant growth and development depend on leaf photosynthetic assimilation and root absorption, making leaves and roots key to revealing plant drought adaptation strategies.

Drought stress causes desert plants to reduce leaf area, close stomata, and decrease photosynthetic rates to minimize water loss while increasing leaf thickness and root length and accumulating functional substances like proline, soluble sugars, and malondialdehyde to enhance drought resistance. However, drought also leads to reactive oxygen species accumulation, affecting physiological metabolic functions. Above- and below-ground physiological-ecological processes are not independent but closely interconnected under drought conditions. Research on plant trait relationships in Inner Mongolian grasslands found that above- and below-ground organs can change synergistically to adapt to environmental changes. Nevertheless, leaf and root functional traits and their coupling relationships also vary with environmental stress intensity and growth stage. Current research on plant water adaptation strategies in extremely arid regions has primarily focused on leaves, with less attention to desert plant root traits and their coordinated changes with leaves.

Alhagi sparsifolia is a perennial leguminous herb and typical desert deep-rooted plant widely distributed in the southern margin of the Taklamakan Desert, playing an important role in sand control and ecological restoration in this region. Numerous scholars have systematically studied the dry matter content, morphological characteristics, root distribution, and drought and saline-alkali resistance of perennial *A. sparsifolia* seedlings. However, research on the functional traits of above- and below-ground organs and their correlations under drought stress remains relatively limited. This study used a controlled pot experiment to simulate drought stress, establishing well-watered, mild stress, and severe stress treatments to analyze changes in leaf and root functional traits and physiological responses under different water conditions. The objective was to explore the water adaptation strategies of *A. sparsifolia* seedlings and provide a scientific basis for vegetation restoration and reconstruction in the Cele oasis-desert transition zone.

1.1 Study Area

The experiment was conducted at the Cele National Station of Observation and Research for Desert Grassland Ecosystem, Chinese Academy of Sciences (80°03 E–82°10 E, 35°17 N–39°30 N). Located in the oasis-desert transition zone on the southern edge of the Taklamakan Desert, the study area features a typical continental arid climate with an average annual precipitation of only 35.1 mm and annual pan evaporation of 2600 mm. Strong winds prevail, with 136 windy days and 39 sandstorm days annually. Soils are primarily aeolian sandy soils with poor water-holding capacity. Vegetation in the oasis depends mainly on summer floods and groundwater for survival. Due to frequent wind-sand activity and high summer temperatures, environmental conditions are harsh, with sparse vegetation cover of only 10%–20%. Dominant plants include the perennial herb *Alhagi sparsifolia*, accompanied by *Karelinia caspica* and a small number of *Tamarix ramosissima* and *Populus euphratica*.

1.2 Experimental Design

The pot experiment used polyethylene threaded tubes (30 cm diameter × 60 cm height) as containers with sealed bottoms. Soil was collected from the 0–30 cm layer of desert areas outside the Cele oasis, with a bulk density of 1.35 $\mathrm{g \cdot cm^{-3}}$, and total nitrogen, phosphorus, and potassium contents of 0.22 $\mathrm{g \cdot kg^{-1}}$, 0.62 $\mathrm{g \cdot kg^{-1}}$, and 16.27 $\mathrm{g \cdot kg^{-1}}$, respectively. Each pot contained 3.31 kg of soil and was thoroughly watered before sowing. Seeds were soaked in warm water before planting at a depth of 0.5 cm, with 20 seeds sown per pot. Before treatment establishment, seedlings were uniformly managed to maintain moist soil conditions. When seedlings reached 3–4 leaves, they were thinned to one plant per pot based on uniform growth.

Previous studies found that the soil water content threshold for *A. sparsifolia* seedling survival was 30%–35% of maximum field capacity. Based on this, three water gradients were established: (1) Control (CK): soil water content at 70%–75% of field capacity; (2) Mild drought stress (W1): 50%–55% of field capacity; and (3) Severe drought stress (W2): 25%–30% of field capacity. Water treatments began on May 20, 2021, with five replicates per treatment. Throughout the growing season, soil water content was measured every 2 days using a TDR300 soil moisture meter (Soil Moisture Equipment, Santa Barbara). Water loss was calculated and replenished to maintain each treatment within its target range, with watering fixed at 19:00 Beijing time.

1.3 Sample Collection and Measurements

1.3.1 Sample Collection Samples were collected during early growth (July 15, 2021) and late growth (September 15, 2021), with three replicates per treatment. For each replicate, 10 intact mature leaves were randomly collected, weighed in the laboratory, and used for leaf morphological measurements. Additional fresh mature leaves were collected and stored at -20 °C for physiological measurements. The remaining aboveground parts were separated into leaves, stems, and thorns, weighed, and oven-dried at 75 °C to constant weight. Roots were extracted using 0.15 mm mesh screens, scanned, and 0.5 g of fresh roots were stored at -20 °C for physiological measurements, with the remaining roots oven-dried and weighed.

1.3.2 Morphological and Biomass Measurements Leaf fresh weight was obtained using a 0.01 g precision balance. Leaf thickness was measured at three points (tip, middle, avoiding main veins) using a 0.01 mm electronic caliper and averaged. Leaves were scanned and analyzed using ImageJ software to obtain leaf area. Scanned leaves were oven-dried at 75 °C to constant weight for leaf dry weight. Specific leaf area (SLA) was calculated as leaf area divided by leaf dry weight. Leaf tissue density (LTD) was calculated as leaf dry weight divided by leaf volume. Leaf dry matter content (LDMC) was calculated as leaf dry weight divided by leaf fresh weight.

Roots were scanned and analyzed using WinRHIZO Pro software to obtain root length, root surface area (RSA), and root volume. Specific root length (SRL) was calculated as root length divided by root dry weight. Root tissue density (RTD) was calculated as root dry weight divided by root volume. Root-shoot ratio (R/S) was calculated as belowground biomass divided by aboveground biomass.

1.3.3 Physiological Measurements Proline, soluble sugar, and malondialdehyde (MDA) contents in leaves and roots were measured following Li Hesheng's methods. Proline content was determined using acidic ninhydrin colorimetry, soluble sugar content by anthrone colorimetry, and MDA content by thiobarbituric acid method.

1.4 Data Analysis

Statistical analysis was performed using SPSS 16.0. One-way ANOVA was used to analyze biomass, morphological traits, and physiological parameters of leaves and roots under different water treatments, with results expressed as means ± standard deviation (95% confidence interval). Multiple comparisons were conducted using Duncan's test. Pearson correlation coefficients were calculated to analyze relationships among traits. Graphs were prepared using Origin 2018 and GraphPad Prism 8.0.1.

Results

2.1 Effects of Drought Stress on Biomass Accumulation in *A. sparsifolia* Seedlings

Drought stress significantly affected biomass accumulation in *A. sparsifolia* seedlings ($P < 0.05$), with all biomass components showing the trend CK > W1 > W2 across both growth stages. During early growth, aboveground biomass accounted for 48.90% and 27.46% of total biomass in CK and W1 treatments, respectively, while belowground biomass was 74.08% and 45.91% in W2. In late growth, although all biomass components decreased with reduced water availability, belowground biomass exceeded aboveground biomass across treatments. The root-shoot ratio increased significantly with decreasing water availability during both early and late growth stages ($P < 0.05$). Although drought inhibited overall seedling growth, the belowground growth capacity was enhanced under drought stress.

2.2 Effects of Drought Stress on Morphological Traits of *A. sparsifolia* Seedlings

Drought stress effects on leaf area, leaf tissue density, and leaf dry matter content varied by growth stage ($P < 0.05$). Leaf area showed no significant differences among treatments during early growth but decreased significantly under W2 during late growth ($P < 0.05$). Leaf tissue density and leaf dry matter content increased with drought intensity, being significantly higher under W2 than other treatments. Specific leaf area showed no significant changes across treatments.

Root morphological traits also changed significantly under drought stress ($P < 0.05$), with different patterns between growth stages. During early growth, root length and surface area decreased significantly under W2 ($P < 0.05$), while specific root length increased significantly ($P < 0.05$). Root tissue density showed the opposite trend, being significantly higher under W1 than CK and W2. During late growth, root length was lowest under W2 and significantly lower than CK ($P < 0.05$). Drought significantly reduced root surface area ($P < 0.05$), with no significant change under W1 but significant increase under W2 ($P < 0.05$). Root tissue density was unaffected by water changes.

[Figure 1: see original paper]
[Figure 2: see original paper]

2.3 Changes in Osmotic Adjustment Substances and MDA in Leaves and Roots Under Drought Stress

Drought stress significantly increased leaf proline and MDA contents ($P < 0.05$). During early growth, leaf proline content under W2 was 341.72% higher than CK, while MDA was 228.57% higher. Soluble sugar content showed no significant changes. During late growth, leaf soluble sugar decreased significantly under W2 ($P < 0.05$), being 30.77% lower than CK. Leaf proline remained significantly higher under W2 ($P < 0.05$), while MDA decreased compared to early growth. Comparing between stages, leaf area decreased by 135.29% under W2, while specific leaf area and leaf tissue density increased by 100.67% and 30.63%, respectively. Proline and MDA contents decreased during late growth under W2.

Root osmotic adjustment substances and MDA showed different patterns between growth stages. During early growth, root soluble sugar and proline followed similar patterns as leaves, with no significant differences in soluble sugar among treatments. Proline increased significantly with stress intensity but was lowest under W2, significantly lower than CK. During late growth, root proline showed no significant differences among treatments, while MDA was significantly higher under W2 than CK and W1. Soluble sugar showed the trend CK > W2 > W1, with significant differences among treatments ($P < 0.05$).

[Figure 3: see original paper]
[Figure 4: see original paper]

2.4 Relationships Between Leaf and Root Traits in *A. sparsifolia* Seedlings

Pearson correlation analysis revealed strong coupling relationships among root traits and between leaf and root traits, while coupling among leaf traits was relatively weak. Leaf trait coupling mainly showed: leaf tissue density was significantly positively correlated with leaf proline content ($P < 0.05$) and extremely significantly positively correlated with leaf dry matter content ($P < 0.01$); specific leaf area was extremely significantly negatively correlated with leaf dry matter content ($P < 0.01$) and significantly negatively correlated with leaf soluble sugar content ($P < 0.05$); leaf area was extremely significantly negatively correlated with leaf proline ($P < 0.01$).

Strong coupling existed between root morphological and physiological traits, with osmotic adjustment substances showing significant correlations with root length, specific root length, and root surface area. Root tissue density was significantly negatively correlated with root length, specific root length, and root surface area. Root physiological traits showed trade-offs with leaf morphology and leaf dry matter content, while parallel relationships existed with leaf soluble sugar content, MDA, and specific leaf area. Leaf and root osmotic adjustment substances showed significant synergistic relationships.

[Figure 5: see original paper]

Discussion

3.1 Effects of Drought Stress on *A. sparsifolia* Seedling Growth

Biomass accumulation directly reflects plant nutrient allocation and physiological-ecological processes, serving as an important indicator of plant productivity and a key strategy for adapting to stressful environments like drought. Biomass allocation represents the process of resource distribution to various organs and reflects plant survival trade-offs. Numerous studies have found that low soil water content significantly inhibits dry matter formation but enhances drought resistance by increasing belowground biomass allocation. Consistent with previous research, this study found that all biomass components of *A. sparsifolia* seedlings decreased significantly with increasing drought severity, likely because drought weakened aboveground photosynthesis, limiting overall dry matter accumulation.

During late growth, belowground biomass exceeded aboveground biomass, and root-shoot ratio increased significantly with water stress. This increased root-shoot ratio enhanced water and nutrient acquisition capacity, while reduced aboveground biomass effectively prevented excessive water loss. This biomass allocation strategy aligns with the drought resistance strategies of most plants.

3.2 Morphological and Physiological Responses of *A. sparsifolia* Seedlings to Drought Stress

Leaves and roots are primary resource acquisition organs with strong plasticity, and their functional traits directly reflect photosynthetic carbon fixation and resource acquisition capacity, closely relating to plant adaptation strategies. Under drought stress, plants often control stomatal closure to maintain water balance and allocate more photosynthates to dry matter accumulation to maintain normal cellular function. *A. sparsifolia* seedlings reduced leaf area to decrease transpiration water loss and increased leaf tissue density and leaf dry matter content during late growth, likely strengthening leaf toughness and compactness to improve defense capacity. This result aligns with drought adaptation strategies observed in other plants.

Although specific leaf area did not change significantly with drought stress, it decreased to some extent during late growth, indicating reduced aboveground resource acquisition capacity. Roots, as resource organs directly contacting soil, are highly sensitive to soil water and nutrient changes. Desert plants typically have extensive root systems to acquire water and nutrients under water deficit conditions. This study found that root length, surface area, and tissue density decreased significantly under drought, while specific root length increased significantly. This indicates that low soil water content limited root biomass accumulation but enhanced resource acquisition capacity through increased specific root length and root tissue density, slowing drought-induced damage.

MDA, a product of cellular peroxidation, directly reflects cell damage and plant drought resistance. With prolonged stress, MDA content increases. This study found that leaf MDA increased gradually with stress intensity during early growth, while root MDA decreased. During late growth, leaf MDA showed no significant change while root MDA increased significantly. These inconsistent changes between leaf and root traits indicate that above- and below-ground organs face different pressures and environments, while stronger trade-off relationships exist between leaf and root traits.

3.3 Adaptive Strategies of *A. sparsifolia* Seedlings Under Water Stress

Above- and below-ground growth and physiological metabolic processes are closely related, and functional traits are not independent but interactively regulate environmental adaptation to generate optimal trait combinations. Studies suggest that specific leaf area and leaf dry matter content represent an optimal combination for resource utilization and adaptation, where increased leaf dry matter content and decreased specific leaf area reduce water loss. *A. sparsifolia* showed trade-offs between specific leaf area and both leaf dry matter content and leaf tissue density, indicating effective maintenance of balance among water loss, dry matter accumulation, and defense capacity.

Leaf and root morphological and osmotic substances showed coupling relationships, indicating that after sensing stress, leaves and roots can regulate growth and physiological metabolism balance to maintain drought resistance. Parallel relationships existed among osmotic adjustment substances, peroxidation products, specific leaf area, and specific root length, suggesting integrated physiological metabolism and resource acquisition processes. As belowground osmotic adjustment capacity and drought resistance enhanced, aboveground light resource acquisition and photosynthetic capacity relatively weakened, reflecting trade-offs between core traits related to leaf morphology and root physiology. This highlights the inseparable nature of above- and below-ground growth.

Integrating all trait changes, although overall growth and development were restricted by drought, *A. sparsifolia* invested more resources in roots than leaves. By regulating root growth to enhance water and nutrient acquisition and defense capacity, and storing dry matter and nutrients to maintain aboveground growth, while aboveground parts appropriately reduced water loss to provide favorable conditions for belowground growth. This adaptive strategy is closely related to self-protection and adaptability in extremely arid environments.

Conclusion

This study investigated the effects of drought stress on leaf and root morphology, physiology, and biomass accumulation in *A. sparsifolia*, yielding the following conclusions:

1. *A. sparsifolia* enhanced leaf compactness and reduced water consumption by decreasing leaf area and increasing leaf tissue density and dry matter content.
2. Drought conditions stimulated MDA accumulation in leaves and roots, damaging cell membranes.
3. Under drought stress, increased specific root length and root proline content enhanced root resource acquisition and osmotic adjustment capacity.
4. The root-shoot ratio of *A. sparsifolia* seedlings increased significantly during late growth, especially under severe drought. Long-term drought stress caused *A. sparsifolia* to concentrate more dry matter investment in root resource acquisition and stress resistance construction, demonstrating an overall slow-investment, conservative growth adaptive strategy under drought stress.

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