# Response of Leaf and Root Morphological Characteristics of *Salsola passerina* Seedlings to Drought Stress (Postprint)

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**Date:** 2024-03-01T00:00:00+00:00

## Abstract

Abstract: Investigating the responses of leaf and root morphological traits of desert plants to drought stress facilitates understanding and predicting the growth regulation strategies of desert plants under climate change conditions. This study employed seedlings of the typical desert plant Caroxylon passerinum as the research subject, established two treatments of slow drought and rapid drought, measured morphological indicators related to leaves and roots, and analyzed the morphological characteristics of leaves and roots of C. passerinum seedlings under different drought stresses and the relationships between them. The results showed that: (1) With prolonged drought stress duration, coarse root diameter decreased under both treatments, specific root length and specific root area of fine roots decreased under rapid drought treatment, while leaf tissue density increased under rapid drought treatment; coarse root tissue density overall increased after slow drought treatment, while rapid drought treatment exhibited an initial increase followed by a decrease. (2) At the end of the growth period (54 d), coarse root diameter significantly decreased under both treatments; succulence degree and water content under rapid drought treatment were significantly lower than those of the control and slow drought treatment, respectively; at 37 d of stress, coarse root tissue density of C. passerinum under both drought treatments significantly increased, and was greater under slow drought than under rapid drought. (3) Coarse root specific root length, coarse root tissue density, fine root specific root length, and specific leaf area were the main indicators of trait variation in C. passerinum; correlation analysis revealed that there were 29 pairs of correlated traits between leaves and roots of C. passerinum. In summary, leaves, coarse roots, and fine roots of C. passerinum all exhibited different adaptive strategies under different water treatments; under both drought treatments, C. passerinum responded to drought stress by reducing coarse root diameter. Under rapid drought conditions, C. passerinum adapted to soil water deficit by increasing leaf tissue density and reducing fine root specific root length and specific root area. C. passerinum adapted to drought through synergistic or trade-off strategies within leaf and root traits, and between leaf and root traits.

## Full Text

# Morphological Characteristics of Leaves and Roots of *Caroxylon passerinum* Seedlings in Response to Drought Stress

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### Abstract

Investigating the responses of leaf and root morphological characteristics of desert plants to drought stress is crucial for understanding and predicting their growth regulation strategies under climate change scenarios. Using seedlings of the typical desert plant *Caroxylon passerinum*, this study implemented two drought treatments—slow drought and rapid drought—to measure relevant morphological indices of leaves and roots, and analyzed the morphological characteristics of leaves and roots and their interrelationships under different drought stress conditions. The results demonstrated that: (1) With extended drought stress duration, thick-root diameter decreased under both treatments; specific root length and specific root area of fine roots decreased under rapid drought; leaf tissue density increased under rapid drought; thick-root tissue density increased overall under slow drought but showed an initial increase followed by a decrease under rapid drought. (2) At the end of the growth period (54 days), thick-root diameter decreased significantly under both treatments; the degree of succulence and water content under rapid drought were significantly lower than those of the control and slow drought treatments, respectively. After 37 days of stress, thick-root tissue density of *C. passerinum* seedlings increased significantly under both drought treatments, with a greater increase under slow drought than under rapid drought. (3) Thick-root specific root length, thick-root tissue density, fine-root specific root length, and specific leaf area were the main indicators of trait variation in *C. passerinum*. Correlation analysis revealed 29 pairs of interrelated traits between leaves and roots. In conclusion, the leaves, thick roots, and fine roots of *C. passerinum* exhibited distinct adaptive strategies under different water treatments. Under both drought treatments, *C. passerinum* responded to drought stress by reducing thick-root diameter. Under rapid drought conditions, *C. passerinum* adapted to soil water deficit by increasing leaf tissue density and reducing fine-root specific root length and specific root area. *Caroxylon passerinum* seedlings adapted to drought through coordinated or trade-off strategies within and between leaf and root traits.

**Keywords:** drought stress; morphological characteristics; leaf; root; *Caroxylon passerinum*

# 1. Materials and Methods

## 1.1 Materials and Cultivation

In May 2021, several *C. passerinum* seedlings approximately 10 cm in height were selected from the piedmont Gobi in Jingtai County, Gansu Province, for transplantation. This region has a temperate arid continental climate (104°43 E, 36°43 N) with a frost-free period of approximately 141 days, average annual wind speed of 3.5 $\mathrm{m \cdot s^{-1}}$, average annual rainfall of 184 mm, and average annual temperature of 9.0 °C. The main soil types are diluvial gray-brown desert soil and sierozem. Zonal vegetation includes *Reaumuria songarica*, *C. passerinum*, *Nitraria tangutorum*, *Neotrinia splendens*, *Kalidium foliatum*, among others. After selection, seedlings were excavated and transported to the experimental base of Gansu Agricultural University for potting, with one plant per pot. The pots had an upper diameter of 38 cm, lower diameter of 30 cm, and height of 18 cm. The cultivation substrate consisted of sandy loam and perlite mixed at a 10:1 ratio, with a field capacity of 17.41%. After seedlings established, drought resistance experiments were conducted in May 2021 by controlling soil water content. Every two days at 18:00, manual weighing and water replenishment were performed to maintain the required soil water content for each treatment. Seedlings were cultivated in a rain shelter at the experimental site of Gansu Agricultural University. The shelter was made of transparent material for rain protection only, without affecting light and ventilation. The shelter had no surrounding obstructions, providing adequate light and ventilation.

## 1.2 Experimental Design

This experiment established one control group (full water supply) and two treatment groups (slow drought and rapid drought), with 10 replicates per treatment, totaling 30 pots (sample size n=10). A randomized block design was used, with experimental materials divided into three plots according to different water treatments, with 50 cm intervals between plots. All experimental seedlings received normal water management, with soil water content maintained at 75%$±5±5±5±5±5±$2% of field capacity.

## 1.3 Index Measurement and Calculation

Sampling was conducted at 7, 15, 27, 37, and 54 days after drought stress initiation, with three plants sampled per treatment each time. During sampling, whole *C. passerinum* seedlings were removed from pots, ensuring maximum root system integrity. Roots were wrapped in plastic film to prevent water loss, and samples were quickly transported to the laboratory. Leaves and roots were separated, and impurities were removed. Leaves were weighed to obtain fresh leaf weight. A vernier caliper was used to distinguish thick roots (diameter >2 mm) and fine roots (diameter $ $2 mm). Leaves, thick roots, and fine roots were then scanned using a scanner (RhIZO 2008a) to obtain leaf surface area, leaf volume, root length, root diameter, root surface area, and root volume. After measurement, leaves and roots were placed in separate envelopes and put in an oven at 105 °C for 30 minutes to deactivate biological activity, then dried to constant weight at 75 °C, after which each part was weighed to obtain dry weight. Indices were calculated as follows: degree of succulence (Suc) = leaf fresh weight/leaf dry weight × 100%; specific leaf area (SLA) = leaf surface area/leaf biomass; leaf tissue density (LTD) = leaf biomass/leaf volume; specific root area (SRA) = root surface area/root biomass; specific root length (SRL) = root length/root biomass; root tissue density (RTD) = root biomass/root volume.

### 1.4 Data Processing

SPSS 26.0 software was used for statistical analysis. Repeated measures ANOVA was employed to examine the effects of drought intensity, drought time, and their interactions on morphological characteristics of *C. passerinum*, with least significant difference (LSD) tests used to examine significant differences in morphological characteristics under the same stress time or intensity. The factoextra package was used to rank the importance of the first four principal component axes. All other figures were generated using R 4.2.1, with data presented as mean ± standard error.

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## 2. Results

### 2.1 Leaf Morphological Characteristics of *C. passerinum* Under Drought Stress

Repeated measures ANOVA indicated (Table 1) that drought intensity had significant effects on leaf water content of *C. passerinum* seedlings ($P<0.05$); drought time had extremely significant effects on leaf succulence degree and water content ($P<0.01$); the interaction between drought intensity and drought time had extremely significant effects on leaf water content but no significant effects on specific leaf area. As shown in Figure 1, with extended drought time, leaf succulence degree and water content of *C. passerinum* seedlings under full water supply and both drought treatments showed decreasing trends. Compared with the initial drought stage (7 days), at the end of the growth period (54 days), succulence degree and water content under full water supply, slow drought, and rapid drought treatments decreased significantly by 54.013%, 46.486%, 80.412% and 15.716%, 11.708%, 57.647%, respectively. With extended drought time, leaf tissue density of *C. passerinum* seedlings under rapid drought treatment increased overall, with a 32.732% increase at the end of the growth period (54 days) compared with the initial stage (7 days). At the end of the growth period (54 days), succulence degree and water content under rapid drought treatment were significantly lower than those under full water supply and slow drought treatments ($P<0.05$). Compared with full water supply, succulence degree and leaf water content decreased by 56.890% and 37.931%, respectively; compared with slow drought, they decreased by 52.218% and 37.363%, respectively.

### 2.2 Thick Root Morphological Characteristics of *C. passerinum* Under Drought Stress

Repeated measures ANOVA results (Table 1) showed that drought intensity had significant effects on thick-root specific root length of *C. passerinum* seedlings ($P<0.05$) and extremely significant effects on thick-root tissue density and thick-root specific root area ($P<0.01$). Drought time had extremely significant effects on thick-root specific root length, thick-root tissue density, and thick-root specific root area. The interaction between drought intensity and drought time had extremely significant effects on thick-root diameter. As shown in Figure 2, with extended drought time, thick-root specific root length and specific root area of *C. passerinum* seedlings under both treatments showed a trend of initial decrease followed by stabilization. Compared with the initial drought stage (7 days), at 37 days, thick-root specific root length and specific root area under both treatments decreased significantly by 36.656% and 51.333%, respectively. With extended drought time, thick-root tissue density of *C. passerinum* seedlings under slow drought treatment showed an increasing trend, with a 39.407% increase at the end of the growth period (54 days) compared with the initial stage (7 days), while thick-root tissue density under rapid drought treatment showed a fluctuating trend, with a 56.132% increase at 37 days compared with the initial stage. With extended drought time, thick-root diameter under full water supply showed an increasing trend, with a 16.787% increase at the end of the growth period (54 days) compared with the initial stage (7 days). In contrast, at 37 days of drought, thick-root diameter of *C. passerinum* seedlings under both treatments showed an overall decreasing trend, decreasing by 41.695% and 40.398%, respectively. At 37 days, thick-root specific root length and specific root area under rapid drought treatment were significantly lower than those under full water supply ($P<0.05$), decreasing by 40.910% and 31.761% compared with full water supply. At 54 days, thick-root tissue density of *C. passerinum* seedlings under full water supply and both drought treatments showed significant differences ($P<0.05$), following the pattern: rapid drought > slow drought > full water supply. Compared with full water supply, the two drought treatments increased by 47.277% and 48.147%, respectively.

### 2.3 Fine Root Morphological Characteristics of *C. passerinum* Under Drought Stress

Repeated measures ANOVA results (Table 1) showed that drought intensity had extremely significant effects on fine-root specific root length and fine-root diameter of *C. passerinum* seedlings ($P<0.01$) and significant effects on fine-root tissue density ($P<0.05$). Drought time had extremely significant effects on fine-root specific root length, fine-root specific root area, fine-root tissue density, and fine-root diameter. The interaction between drought intensity and drought time had extremely significant effects on fine-root specific root length, fine-root specific root area, fine-root tissue density, and fine-root diameter. As shown in Figure 3, with extended drought time, fine-root specific root length and specific root area of *C. passerinum* seedlings under rapid drought treatment showed an overall decreasing trend. Compared with the initial drought stage (7 days), at the end of the growth period (54 days), fine-root specific root length and specific root area under rapid drought treatment decreased by 56.532% and 55.001%, respectively. In contrast, fine-root specific root length and specific root area under slow drought treatment showed a trend of initial decrease (7–15 days) followed by increase (15–54 days). Compared with the initial stage, at 15 days, specific root length and specific root area decreased by 35.198% and 34.674%, respectively, while at 54 days, they increased by 35.182% and 29.794%, respectively. With extended drought time, fine-root tissue density and diameter under full water supply showed increasing trends, with increases of 40.778% and 28.317% at the end of the growth period (54 days) compared with the initial stage (7 days). In contrast, at 15 days of drought, fine-root tissue density and diameter under both drought treatments increased by 34.674% and 16.566%, respectively; at 27 days, they increased by 49.114% and 29.794%; and at 54 days, they increased by 56.532% and 55.001%. At 15 days, fine-root specific root length and specific root area under slow drought treatment were significantly higher than those under full water supply and rapid drought treatments ($P<0.05$), increasing by 48.316% and 37.980% compared with full water supply, and by 36.612% and 22.621% compared with rapid drought. At 27 days, fine-root tissue density under rapid drought treatment was significantly higher than that under full water supply and slow drought treatments ($P<0.05$), increasing by 37.214% compared with full water supply and by 64.660% compared with slow drought.

## 3. Discussion

### 3.1 Effects of Drought Stress on Leaf Morphological Characteristics of *C. passerinum* Seedlings

Changes in leaf morphological traits can reflect the functional characteristics of the ecosystem where plants are located and their adaptability to that ecosystem. Studies have shown that with intensified drought stress, plants can adapt to drought by increasing leaf tissue density and decreasing specific leaf area, leaf water content, and succulence degree. This study found that with extended drought stress time, leaf succulence degree and water content of *C. passerinum* seedlings showed decreasing trends, and at the end of the growth period, succulence degree and leaf water content were lowest under rapid drought treatment, similar to results reported by Zhao Guangxing et al. This indicates that during drought stress, *C. passerinum* seedlings maintain normal physiological activities by consuming water stored in succulent leaves, leading to significant reductions in leaf succulence degree and water content, with rapid drought having the greatest impact. However, other studies have shown that with reduced natural precipitation, leaf succulence degree and water content of *Reaumuria songarica* increased, possibly because *R. songarica* maintains normal growth by increasing succulence to lock in water and maintain normal cell metabolism. This suggests that as soil water decreases and water supply from roots to shoots diminishes, plants respond to this stress by increasing leaf succulence degree and water content to reduce water loss and enhance resource conservation capacity.

Specific leaf area directly reflects plant adaptability to different habitats and resource acquisition capacity. Studies have shown that under drought stress, desert plants adapt to water deficit by decreasing specific leaf area. This study found that extended drought stress time and intensified stress did not affect specific leaf area of *C. passerinum* seedlings. However, this contradicts the findings of Zhang Xi et al. that specific leaf area of *Medicago sativa* decreased with intensified drought stress. This discrepancy may be due to different species or drought gradient settings. Therefore, future in-depth studies on leaf morphological changes under drought stress should consider species selection and drought gradient design comprehensively.

Leaf tissue density is an important indicator for studying stress resistance of desert plants. Plants with higher leaf tissue density grow slowly, can store more carbon for defense structures, and retain more water and nutrients to adapt to arid habitats. In this study, with extended drought stress time, leaf tissue density of *C. passerinum* seedlings under rapid drought treatment showed an increasing trend, similar to Shipley’ s findings that plants in arid regions adapt to drought stress by increasing leaf tissue density. This indicates that under rapid drought treatment, *C. passerinum* forms adaptations to drought stress by increasing leaf tissue density with extended stress time. However, this contradicts Xu Min’ s findings that *Buddleja officinalis* resisted drought stress with lower leaf tissue density, possibly because plants in desert habitats and karst rocky desertification habitats have specific drought resistance characteristics when coping with soil water deficit, which may be related to their genetic traits.

### 3.2 Effects of Drought Stress on Root Morphological Characteristics of *C. passerinum* Seedlings

Root morphological characteristics directly affect the growth and development of aboveground plant parts. Fine roots are the most active part of the root system for absorbing soil water and nutrients, with highly divisible and metabolically active root tip cells. In contrast, thick roots are less sensitive to soil water and nutrient supply. Specific root length and specific root area are important indicators reflecting root morphological structure and comprehensively reflect plant water and nutrient absorption capacity and ecological adaptability. Studies have shown that with increased drought intensity, plant specific root length and specific root area decrease. Other research suggests that water stress increases specific root length and specific root area of *Reaumuria soongorica* seedlings, mainly through lower-order roots. This study found that under different treatments, with extended drought stress time, thick-root specific root length and specific root area of *C. passerinum* seedlings showed an overall trend of initial decrease followed by stabilization; fine-root specific root length and specific root area showed continuously decreasing trends under rapid drought treatment, while under slow drought treatment they showed a trend of initial decrease followed by increase. However, this contradicts findings by Li Shuai et al. and Huang Haixia et al., possibly because after initial exposure to slow drought stress, fine roots respond to water stress by decreasing specific root length and specific root area, then through self-regulation increase fine-root specific root length and specific root area to expand root growth space and adapt to drought. Thick roots basically adapt to the drought environment after a period of drought stress, with specific root length and specific root area remaining relatively stable. This suggests that fine-root specific root length and specific root area of *C. passerinum* seedlings may be more sensitive to drought treatments than thick roots, and that moderate drought stress intensity and extended drought duration are beneficial for improving water and nutrient resource acquisition capacity of *C. passerinum* seedlings.

Plants with greater root tissue density have stronger root tissue defense and extension capacity, which is more advantageous for acquiring water and nutrients. This study found that with intensified drought stress and extended drought time, thick-root tissue density of *C. passerinum* seedlings increased overall, but decreased in the later stage of rapid drought stress, while fine-root tissue density showed an overall trend of initial decrease followed by increase from a certain point in drought stress to the end of the stress period. However, this contradicts Sun Jingjue’ s finding that plant fine-root tissue density increases with reduced water in the habitat. This may be because decreasing root tissue density can accelerate plant growth turnover, reduce water and nutrient loss, and improve water and nutrient use efficiency. However, after *C. passerinum* seedlings adapt to drought conditions, they increase fine-root tissue density through self-regulation, which strengthens fine-root toughness and defense, compensating for risks associated with root thinning and elongation during drought. This indicates that moderate drought stress intensity and duration are beneficial for expanding plant root defense and improving material storage capacity and drought tolerance, meaning *C. passerinum* can achieve maximum growth benefits under slow drought conditions. However, thick-root drought tolerance decreases after rapid drought stress.

Root diameter affects the ability of roots to anchor plants in soil and absorb water and nutrients, reflecting root development in space. Some studies suggest that plants can form different stress avoidance strategies to adapt to drought by utilizing coordinated or trade-off relationships among morphological traits. This study found that with extended stress time, thick-root diameter of *C. passerinum* seedlings under both slow and rapid drought treatments showed an overall decreasing trend, while fine-root diameter showed a trend of initial decrease followed by increase. This is similar to findings by Zhang Jinju et al. that average root diameter of *Lycium ruthenicum* seedlings decreased initially then increased with intensified drought stress. This indicates that within a certain drought stress period, root diameter of *C. passerinum* seedlings decreased to varying levels after drought treatment. However, in the middle and late stages of drought stress, fine-root diameter increased, possibly because drought stress hindered thick-root growth and development, leading to increased fine-root numbers that facilitated fine-root growth. This suggests that with extended drought stress time, plants regulate fine-root growth by reducing thick-root growth, meaning plants can make corresponding survival strategies in response to water stress through trade-offs among their own traits under drought conditions.

### 3.3 Relationships Between Root and Leaf Morphological Traits

Principal component analysis of leaf and root morphological traits of *C. passerinum* seedlings revealed no clear separation of *C. passerinum* individuals under different water treatments along the first or second principal component axes, indicating that it is difficult to identify specific trait combinations related to drought resistance in *C. passerinum* under different drought stress conditions. However, importance ranking of morphological traits in this study identified thick-root specific root length, thick-root tissue density, fine-root specific root length, and specific leaf area as the main indicators affecting trait variation in *C. passerinum*. This suggests that *C. passerinum* can adapt to soil water changes in the environment by regulating these indicators. However, this contradicts findings by Zhou Jie et al. on drought adaptation strategy differences in *Alhagi sparsifolia*, possibly because specific leaf area and specific root length are important indicators characterizing plant adaptation to different habitats and resource acquisition capacity, while root tissue density is a root morphological indicator characterizing plant defense and absorption capacity. The discrepancy may also be related to species characteristics or different adaptation strategies formed by different plants under different water environmental conditions. Therefore, further research in this area can provide reference for understanding plant morphological adaptation under drought stress.

Studies have shown that plant functional traits are not independent when functioning, but rather exhibit certain correlations among traits. This study found that leaf and root morphological traits of *C. passerinum* seedlings showed varying degrees of correlation within each trait system. Specifically, succulence degree showed significant positive correlations with leaf water content, specific leaf area, thick-root specific root area, and thick-root specific root length, indicating that under different water stress conditions, *C. passerinum* seedlings respond to drought stress through coordinated variation between leaves and thick roots. The possible reason is that in water-stressed habitats, *C. passerinum* seedlings form drought tolerance strategies by increasing leaf water retention capacity and strengthening xeromorphic characteristics of thick roots. This study also found that leaf water content showed extremely significant negative correlations with leaf tissue density, fine-root specific root length, and fine-root specific root area. This is consistent with results reported by Ma Li et al., indicating that *C. passerinum* seedlings respond to drought stress through trade-off strategies between leaves and fine roots. The possible reason is that under drought stress conditions, as leaf water content decreases, plants increase leaf tissue density to prevent excessive water loss from leaves. Moreover, with intensified drought stress, fine-root tip cells divide vigorously, increasing fine-root length and biomass, thereby increasing fine-root specific root length and specific root area and enhancing water and nutrient acquisition and utilization capacity of *C. passerinum* seedlings. This study also found a negative correlation between fine-root specific root length and thick-root tissue density, which differs from Qi Dehui' s findings of negative correlation between fine-root specific root length and fine-root tissue density under different water gradients. This may be because under drought conditions, *C. passerinum* seedlings prioritize fine-root growth, leading to hindered thick-root growth and decreased thick-root defense function, indicating that *C. passerinum* seedlings respond to water stress by trading off relationships among root morphological characteristics.

## 4. Conclusion

Through investigating the response of leaf and root morphological characteristics of *C. passerinum* seedlings to drought stress, this study found that drought stress hindered thick-root growth. Under slow drought conditions, fine-root specific root length and specific root area decreased while thick-root tissue density increased, whereas under rapid drought treatment, thick-root tissue density showed an initial increase followed by a decrease. The degree of succulence and water content under rapid drought treatment were significantly lower than those under full water supply and slow drought treatments. Under rapid drought treatment, *C. passerinum* adapted to the arid environment by increasing leaf tissue density to construct a defense system that preserves internal nutrients. Moderately extending drought duration and increasing drought stress intensity were more conducive to enhancing water and nutrient resource acquisition and root defense function in *C. passerinum* seedlings. *Caroxylon passerinum* seedlings adapted to arid habitats through coordinated or trade-off strategies within and between leaf and root traits. Under different drought treatments, *C. passerinum* did not exhibit specific trait combinations to form drought resistance strategies.

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