Effects of Altered Rainfall Patterns on Root Morphological Characteristics of Nitraria Seedlings (Postprint)

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Abstract

To investigate the response characteristics of root morphology in desert plant Nitraria seedlings to changes in rainfall patterns, a controlled simulation experiment was conducted with three rainfall gradients (W-, W, W+) and two rainfall interval gradients (T, T+). The results showed that: 1) Rainfall amount and rainfall interval exerted varying degrees of influence on the root morphology of Nitraria seedlings, with rainfall amount having a greater effect; 2) Under the same rainfall amount, extending the rainfall interval decreased taproot length, average root diameter, root volume, and root surface area of Nitraria seedlings, but increased total root length, root biomass, and total biomass; under high rainfall conditions (W+), extending the rainfall interval increased specific root length and specific surface area of Nitraria seedlings by 45.09% and 20.20%, respectively, but the differences were not significant; 3) Under the same rainfall interval, a 30% reduction in rainfall only increased taproot length by an average of 12.06%, while root morphological indices including total root length, average root diameter, root volume, and root surface area all decreased significantly, and specific root length and specific surface area showed little change; a 30% increase in rainfall only caused a significant increase in specific surface area, with no significant differences in other morphological indices; taproot length and root-to-shoot ratio reached their maximum under low rainfall conditions (W-), while other indices reached their maximum under high rainfall conditions (W+); 4) Principal component analysis of eight root morphological parameters revealed that six root ecological parameters—root biomass, total root length, total root surface area, specific root length, specific surface area, and root volume —were significantly affected by rainfall patterns.

Full Text

Preamble

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Response of Root Morphological Characteristics of *Nitraria tangutorum* Seedlings to Precipitation Pattern Changes

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Abstract

Global climate models have predicted changes in precipitation patterns, with extended periods between precipitation events and larger individual precipitation events expected to increase. Furthermore, with global climate change, local rainfall patterns in northwestern China have also changed, showing an increasing trend over the past 80 years. Such altered precipitation regimes will significantly modify the temporal water supply to desert ecosystems, thereby affecting ecological processes and ultimately influencing species composition and biological diversity. Seedling root growth represents the most critical stage in plant regeneration and is the most sensitive phase in the plant life cycle to environmental conditions. The responses of root morphology to precipitation changes and the adaptive capacity of seedlings directly affect subsequent seedling establishment success and may influence regeneration dynamics.

Nitraria tangutorum, a super-xerophytic shrub, exhibits strong tolerance to drought, cold, and saline-alkali soil conditions. As the dominant species in desert vegetation of northwestern China, it serves as a key species for revegetation of arid and semiarid areas. Most previous research has examined the impacts of precipitation amount rather than the combined effects of both precipitation amount and interval on this species.

To understand how climate-driven precipitation changes affect desert plants, particularly the response of root morphology to precipitation pattern changes, we conducted a controlled experiment with two factors: precipitation quantity (natural precipitation as control, 30% reduction, and 30% increase) and precipitation interval (time elapsed between two precipitation events: 5 or 10 days). The results showed that root morphological characteristics were influenced by both total precipitation and precipitation interval, with the former playing a more significant role than the latter.

Under the same precipitation amount, extending the precipitation interval decreased main root length, root diameter, root volume, and root surface area, while increasing total root length, root biomass, and total biomass. In high precipitation conditions, extending the precipitation interval increased specific root length (SRL) and specific root area (SRA) by 45.09% and 20.20%, respectively, though these differences were not significant. For the same precipitation interval, reduced precipitation significantly decreased total root length, diameter, volume, and surface area, while SRL and SRA remained basically unchanged. Main root length increased by an average of 12.06% under reduced precipitation, but the differences were not significant.

In low precipitation conditions, main root length and root-shoot ratio reached maximum values, while other morphological indices showed no significant differences. In high precipitation conditions, total root surface area, SRA, and root volume were largest. Principal component analysis of eight root morphological characteristics revealed that root biomass, total root length, total root surface area, SRL, SRA, and root volume were significantly affected by precipitation pattern changes.

We suggest that the root morphology of *N. tangutorum* seedlings was mainly affected by precipitation amount; however, precipitation interval could be as important as amount for root morphology. Increasing precipitation amount and extending precipitation interval (less frequent but higher volume precipitation events) enhanced root growth and population regeneration.

Keywords: precipitation; precipitation interval; root morphology; *Nitraria tangutorum*

Introduction

Global climate change has altered precipitation patterns in global and regional scales, including precipitation amount, intensity, and seasonal distribution in northwestern China. Climate models predict increased summer rainfall and extreme precipitation events. As the primary water source for desert plants, these changes will inevitably affect plant physiological and ecological processes, ultimately influencing plant community composition in arid desert terrestrial ecosystems.

Previous research has primarily focused on precipitation amount changes rather than temporal distribution patterns (i.e., precipitation regime). Root morphology is an important indicator describing how plant roots respond to environmental changes. Soil moisture variation is a critical factor affecting root morphological characteristics. When soil moisture changes, plant roots first perceive the change and rapidly transmit signals to various organs, altering their morphology and physiological-biochemical properties to adapt to the variable water environment. Precipitation pattern changes most directly affect soil water content, which subsequently changes soil temperature and ultimately influences plant morphology, structure, and physiology.

Previous studies on soil moisture effects on root morphology have yielded inconsistent conclusions. Some found that reduced soil moisture leads to thinner main roots but increased total root length, while others reported that water stress inhibits root expansion and elongation. Some research indicates that mild water stress can promote root growth and increase total root length. These varying responses highlight our limited understanding of how future precipitation pattern changes will affect root morphology adjustments. Strengthening research on root morphology responses to soil moisture changes under different precipitation patterns is ecologically significant for understanding root growth responses and adaptation mechanisms under global climate change.

Nitraria tangutorum is a common dominant constructive species in desert regions of northwestern China. Previous studies have focused on its physiological characteristics, water use efficiency, and community function, with some reports on aboveground morphological responses to artificial rainfall enhancement. However, responses of underground root morphological characteristics to precipitation pattern changes remain unreported. Research indicates that northwestern desert regions show warming and increasing precipitation trends, with varying magnitudes across regions and more intense precipitation fluctuations. The number of consecutive dry days is increasing, with more extreme rainfall events.

As the water absorption organ, roots first perceive precipitation changes. Under future precipitation pattern changes in desert regions, how will the root system of this typical desert plant respond? What impacts will precipitation changes have on seedling regeneration? These questions require further investigation. This study addresses the following scientific questions: (1) Under global warming, will precipitation pattern changes promote or inhibit *N. tangutorum* root growth? (2) How do precipitation amount changes affect root morphological characteristics and biomass allocation in *N. tangutorum* seedlings? (3) How do extended precipitation intervals affect root morphological characteristics? Addressing these questions is important for revealing seedling root growth response mechanisms and predicting evolutionary directions and rates of *N. tangutorum* under future precipitation pattern changes in desert regions.

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1. Experimental Materials

One-year-old container seedlings of *Nitraria tangutorum* were used as experimental materials. The experiment employed a pot culture method with pots having an outer diameter of 38 cm and height of 36 cm. The potting soil was loess soil with a field water-holding capacity of 20.12% and air-dried soil water content of 5.5%. Each pot contained 15 kg of crushed and sieved air-dried soil.

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2. Experimental Design

In early May, *N. tangutorum* seedlings were transplanted into pots and placed in a movable rain shelter for controlled water experiments, with one seedling per pot. Artificial management ensured survival. After seedling establishment, the rain shelter prevented natural precipitation from affecting the seedlings.

According to meteorological data from the Minqin Desert Grassland Ecosystem National Field Scientific Observation and Research Station in northwestern desert regions, precipitation showed an increasing trend from 1961 to 2008 at a rate of 4.462 mm/10a. Precipitation intervals also extended, with light rain (1-10 mm) accounting for 59.55% of annual precipitation and 10–20 mm rainfall accounting for 22.24%. The increase rate of precipitation intensity was most obvious. Consecutive dry days showed an increasing trend, and extreme rainfall events increased.

This experiment set up three precipitation gradients and two precipitation interval gradients, with six replicates per treatment. The precipitation gradients were: natural monthly precipitation as control (W), 30% reduction (W-), and 30% increase (W+). The precipitation interval gradients were: natural precipitation interval consistent with actual rainfall timing (T, 5 days), and increased interval (T+, 10 days). The six treatments were: W-T, W-T+, WT, WT+, W+T, and W+T+.

Precipitation increase or decrease referred to simulated rainfall being increased or decreased by 30% based on natural precipitation amounts. Unchanged precipitation interval meant artificial rainfall timing matched natural rainfall events. Increased precipitation interval meant the timing of the second simulated rainfall event in each month was set to extend the interval between two natural rainfall events, with natural rainfall occurring after this day combined to achieve the purpose of extending precipitation intervals and increasing large rainfall event frequency.

The experiment was conducted at the Gansu Agricultural University experimental field from May to September. Based on each natural rainfall event' s amount, destructive sampling was performed at the end of the growing season (August-September). During the experiment, regular soil loosening, weeding, and pest control were performed to prevent soil compaction.

Experimental precipitation and precipitation interval settings

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3. Sampling and Measurement

At the end of the growing season (August-September), *N. tangutorum* seedlings were collected. During sampling, the pot exterior was gently tapped to separate roots from soil. Main root length was measured with a tape measure, then aboveground and belowground parts were separated at the base diameter. Intact root systems were placed in ziplock bags and taken to the laboratory.

Roots were scanned using a scanner and analyzed with WinRhizo root analysis system to obtain morphological indices: total root length, average root diameter, root volume, and root surface area. Scanned roots were placed in envelopes and oven-dried at 80°C to constant weight to obtain root biomass (RB).

Specific root length (SRL) and specific root area (SRA) were calculated as: - SRL = total root length / root biomass - SRA = root surface area / root biomass

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4. Data Processing

SPSS 17.0 software was used for statistical analysis. One-way ANOVA analyzed precipitation or precipitation interval effects on root morphological characteristics. Two-way ANOVA analyzed interactive effects of precipitation amount and interval. Principal component analysis examined how precipitation amount and interval differences affected root morphological variation. Significance was tested using LSD method at = 0.05. Data in figures are means.

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1. Main Root Length and Total Root Length Under Different Precipitation Patterns

Precipitation amount significantly affected total root length and main root length ($P < 0.05$), while precipitation interval and their interaction had no significant effect on total root length. The interaction between total precipitation and precipitation interval had extremely significant effects on main root length ($P < 0.01$).

Under consistent precipitation amount, extending precipitation interval from 5 to 10 days decreased main root length but increased total root length, though differences were not significant ($P > 0.05$). Large rainfall events improved soil water content and promoted total root length growth in *N. tangutorum* seedlings.

When precipitation interval was consistent, precipitation changes affected main root length and total root length differently. Compared with the control, 30% precipitation reduction significantly decreased total root length by 31.5% ($P < 0.05$) but increased main root length by 1.65%. Precipitation increase (30%, W+T+) resulted in maximum total root length, while main root length significantly increased by 12.06% ($P < 0.05$).

Two-way ANOVA results (F-values) for effects of total precipitation and precipitation interval on main root length, root biomass, total root length, average root diameter, root volume, root surface area, specific root length (SRL), and specific root area (SRA) of *N. tangutorum* seedlings

[Figure 1: see original paper] Dynamics of main root length and total root length of *N. tangutorum* seedlings under different precipitation patterns

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2. Root Average Diameter, Volume, and Surface Area Under Different Precipitation Patterns

Two-way ANOVA revealed that precipitation amount significantly affected root average diameter, volume, and surface area ($P < 0.05$), while precipitation interval and their interaction had no significant effects.

Under the same precipitation amount, extending precipitation interval showed decreasing trends in root average diameter, volume, and surface area. Under the same precipitation interval, precipitation reduction significantly inhibited growth of root average diameter, volume, and surface area. Compared with the control, 30% precipitation reduction significantly decreased root average diameter, volume, and surface area by 31.5%, 38.63%, and 37.84%, respectively ($P < 0.05$). Precipitation increase enhanced root average diameter, volume, and surface area, but differences were not significant ($P > 0.05$).

[Figure 2: see original paper] Dynamics of root volume, average diameter, and surface area of *N. tangutorum* seedlings under different precipitation patterns

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3. Specific Root Length and Specific Surface Area Under Different Precipitation Patterns

Precipitation amount had extremely significant effects on specific surface area ($P < 0.01$), but precipitation interval and their interaction had no significant effects on specific root length or specific surface area.

Under high precipitation conditions (W+), extending precipitation interval significantly promoted increases in specific root length and specific surface area. Under low precipitation conditions (W-), precipitation interval extension had little effect on specific root length and specific surface area.

Under consistent precipitation interval conditions, specific root length and specific surface area showed varied responses to precipitation amount. Under normal precipitation interval (T), they changed little with precipitation amount.

Under extended interval conditions (T+), precipitation increase significantly promoted specific root length and specific surface area, which increased by 17.07% and 19.50% on average, respectively.

[Figure 3: see original paper] Dynamics of specific root length (SRL) and specific root area (SRA) of *N. tangutorum* seedlings under different precipitation patterns

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4. Root Biomass, Total Biomass, and Root-Shoot Ratio Under Different Precipitation Patterns

Precipitation amount significantly affected total biomass and root-shoot ratio ($P < 0.05$) but had little effect on root biomass. Precipitation interval and their interaction had no significant effects on root biomass, total biomass, or root-shoot ratio.

When precipitation interval was consistent, root biomass and total biomass of *N. tangutorum* seedlings generally increased with precipitation amount. Large rainfall events formed by extended precipitation intervals promoted increases in root and total biomass. When precipitation amount was consistent, precipitation reduction significantly inhibited growth of root average diameter, volume, and surface area.

Compared with the control, 30% precipitation reduction decreased total biomass by 27.4% and significantly increased root-shoot ratio ($P < 0.05$), promoting underground root growth, which reached a maximum value of 0.78. Under natural precipitation interval conditions, precipitation reduction caused leaf abscission and significantly decreased aboveground biomass, while underground biomass did not decrease significantly, thus increasing the root-shoot ratio.

[Figure 4: see original paper] Dynamics of root-shoot ratio, root biomass, and total biomass of *N. tangutorum* seedlings under different precipitation patterns

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5. Effects of Precipitation Patterns on *N. tangutorum* Root Morphology

To investigate the overall effects of precipitation patterns on root morphological variation in *N. tangutorum* seedlings, principal component analysis was performed on eight morphological parameters: main root length, average root diameter, root biomass, total root length, total root surface area, specific root length, specific surface area, and root volume.

Three principal components were extracted as effective components, with a cumulative contribution rate of 85.968%. The first principal component was highly positively correlated with root biomass, total root length, and total root surface area. The second principal component was highly positively correlated with specific surface area and specific root length. The third principal component was highly positively correlated with root volume.

These results indicate that root biomass, total root length, total root surface area, specific root length, specific surface area, and root volume are the main parameters of root morphological characteristics under different precipitation patterns.

Principal component loading matrix

Discussion

Adaptive responses of root morphology are fundamental mechanisms for plants to cope with habitat conditions and are sensitive to water changes. When soil moisture changes, plant roots alter their morphology and physiology to adapt. Previous studies show that under drought stress, desert plants particularly extend main root growth to access deep soil water. This study found that shortened precipitation intervals (increased frequency with reduced individual rainfall) promoted main root length growth in *N. tangutorum* seedlings, reaching maximum values under low precipitation conditions.

When precipitation amount is constant, shortened intervals create small rainfall events. In arid desert regions with intense evaporation, small rainfall events rarely form effective soil moisture. *N. tangutorum* adapts by extending main roots to access water sources. The study also found that total root length increased with both precipitation amount and extended intervals, possibly because extended drought periods induced lateral root growth, enhancing drought tolerance, while appropriate precipitation increases stimulated fine root proliferation.

Extreme drought events cause decreased leaf stomatal conductance and even stomatal closure, reducing photosynthetic rates and inhibiting growth. Conversely, increased water availability has opposite effects. This study found that high precipitation conditions produced *N. tangutorum* seedlings with well-developed, densely growing fine roots, while drought stress reduced lateral roots and root hairs, decreasing root biomass and metabolic activity. Appropriate water increases stimulated numerous lateral roots and root hairs, increasing water and nutrient absorption area.

Rainfall effectiveness relates not only to amount but also to interval. This study found that extended precipitation intervals decreased root average diameter, volume, and surface area, contrasting with some previous studies on other species. This may be because long intervals subjected plants to prolonged drought, and alternating long drought periods with increased single rainfall events created greater surface soil moisture fluctuations, potentially increasing runoff losses despite reduced evaporation.

Precipitation reduction significantly decreased root average diameter, volume, and surface area. With prolonged drought, soil microbial activity weakens, nitrogen mineralization rates decrease, and nutrient enrichment followed by sudden release may increase leaching losses, affecting root nutrient and water uptake. Although extended intervals doubled individual rainfall amounts, the compensation effect could not fully recover from long drought damage, only partially alleviating it.

Specific root length and specific surface area correlate with plant growth rhythms and environmental conditions. Plants with larger specific root length and specific surface area have advantages in water and nutrient acquisition. This study found that only under W+T+ treatment did *N. tangutorum* seedlings show greater specific root length and specific surface area, indicating that increased precipitation combined with extended intervals promoted rapid growth.

Root systems first perceive precipitation changes. Precipitation changes alter biomass allocation patterns and growth characteristics, affecting plant establishment in communities. Optimal allocation theory suggests that when water resources decrease, plants reduce aboveground leaf biomass allocation and relatively increase underground biomass allocation. This study found that precipitation reduction increased root-shoot ratio, with plants investing more biomass in roots, consistent with studies on other desert plants and demonstrating adaptation to arid environments.

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