Effects of Different Rainfall Frequencies on Stoichiometric Characteristics of Salsola subcrassa During the Growing Season: Postprint

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Abstract

Under changing precipitation patterns, investigating the stoichiometric characteristics of carbon (C), nitrogen (N), and phosphorus (P) in various plant organs and the construction of nutrient transport pathways facilitates understanding of C, N, and P allocation patterns, which is of significant importance for the survival and persistence of native plants. This study established four precipitation treatments: adding 20 mm water once per month (W1), adding 10 mm water twice per month (W2), adding 5 mm water four times per month (W4), and natural precipitation as a control (CK). We explored the differences in C, N, and P stoichiometric characteristics and the contents of neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) in different organs (leaf, stem, fruit) of the desert plant Salsola subcrassa M. Pop., aiming to reveal the effects of precipitation pattern changes on nutrient acquisition in typical desert plants. The results showed that: (1) Under all precipitation frequencies, with plant growth, the N content in leaves and fruits of Salsola subcrassa gradually decreased, whereas it gradually increased in stems. Compared with CK, the W4 treatment increased the N content in leaves, stems, and fruits throughout the entire growth period; the P content in leaves and stems gradually decreased with plant growth, but gradually increased in fruits. Compared with other treatments, the W4 treatment increased the P content in stems and fruits throughout the growth period. (2) Under all precipitation treatments, the C:N ratios in leaves and stems showed a trend of first increasing and then decreasing over time, while their C:P and N:P ratios gradually increased. The C:N and C:P ratios in fruits remained relatively stable, whereas the N:P ratio in fruits gradually decreased. Compared with other treatments, the W4 treatment significantly increased the N:P ratios in leaves and fruits during the fruit growth period ($P<0.05$). Overall, compared with CK, precipitation treatments at other frequencies all optimized the nutrient allocation strategy of Salsola subcrassa. (3) With plant growth, the contents of NDF, ADF, and ADL in leaves and stems all increased significantly (P<0.05), and leaves showed significant differences under the same treatment across different periods (P<0.05). Compared with other treatments, only the W4 treatment increased the ADF content in stems and fruits during the fruit growth period. In summary, the nutrient allocation of Salsola subcrassa under the W4 treatment was more conducive to promoting plant growth, indicating that this plant is better able to optimize nutrient allocation and complete its life history under high-frequency, low-amount rainfall events.

Full Text

Effects of Different Rainfall Frequencies on the Stoichiometric Characteristics of Salsola subcrassa During the Growth Period

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Abstract

Under changing precipitation patterns, investigating the stoichiometric characteristics of carbon (C), nitrogen (N), and phosphorus (P) in plant organs and the construction of nutrient transmission pathways helps elucidate element allocation rules, which is crucial for the survival and persistence of native plants. This study established four precipitation treatments: 20 mm added once monthly (W1), 10 mm added twice monthly (W2), 5 mm added four times monthly (W4), and natural precipitation as a control (CK). We examined the stoichiometric characteristics of leaves, stems, and fruits of *Salsola subcrassa* M. Pop., a typical desert plant, and analyzed differences in neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) contents to reveal how precipitation pattern changes affect nutrient acquisition. Results showed that under all treatments, N content in leaves and fruits decreased gradually with plant growth, while increasing in stems. Compared with CK, the W4 treatment enhanced N content in leaves, stems, and fruits throughout the growth period. Phosphorus content decreased in leaves and stems but increased in fruits with plant growth; the W4 treatment increased P content in stems and fruits compared to other treatments. Under each precipitation treatment, the C:N ratio in leaves and stems showed a trend of first increasing then decreasing over time, while C:P and N:P ratios increased. In fruits, C:N and C:P ratios remained relatively stable, whereas N:P decreased. The W4 treatment significantly increased

N:P ratios in leaves and fruits during the fruit growth period ($P < 0.05$) compared to other treatments. Overall, treatments other than CK optimized the nutrient distribution strategy of *S. subcrassa*. As plants grew, NDF, ADF, and ADL contents in leaves and stems increased significantly ($P < 0.05$), with leaves showing significant differences under the same treatment across different periods ($P < 0.05$). Only the W4 treatment increased ADF content in stems and fruits during the fruit growth period. These findings indicate that *S. subcrassa* optimizes nutrient distribution more effectively under high-frequency, low-intensity rainfall events.

Keywords: *Salsola subcrassa* M. Pop.; different precipitation frequency; nutrient utilization strategy; ecological stoichiometry

1 Study Area and Methods

1.1 Study Area Overview

The experiment was conducted at the Fukang Station of Desert Ecology, Chinese Academy of Sciences (44°17 N, 87°56 E), located on the southern edge of the Gurbantunggut Desert. The region has a temperate continental arid climate with hot, dry summers and cold winters with stable snowfall. The average annual temperature is approximately 6.6°C, annual precipitation ranges from 70–180 mm, and annual potential evaporation exceeds 1000 mm. Precipitation primarily occurs as mountain runoff, glacial meltwater, and rainfall. Groundwater consists of unconsolidated rock pore water. Soils are predominantly saline gray desert soils or cracked gray desert soils with light loam texture and compaction. *Haloxylon ammodendron* and *Haloxylon persicum* are the dominant species, accompanied by various herbaceous plants including *Atriplex dimorphostegia* and *Salsola nitraria*. *Salsola subcrassa* is an annual herbaceous plant. Based on phenological observations, seedling emergence and growth occur in April–May, flowering and fruiting in June–July, fruit development in August, and seed maturation in September.

1.2 Precipitation Selection

We analyzed precipitation data from 2010–2015 at the Fukang Station (Figure 1) to determine appropriate rainfall amounts. Most rainfall events were $ $5 mm, accounting for the majority of precipitation events. Events of 1-5 mm occurred most frequently, while 10–20 mm events were less common, and 5–10 mm events were rare. The monthly maximum rainfall was approximately 20 mm. Therefore, we selected 5 mm, 10 mm, and 20 mm as experimental rainfall amounts, with 20 mm representing the maximum monthly precipitation.

1.3 Experimental Design

The study was conducted in native saline-alkali land east of the Fukang Station. On April 15, 2017, we selected an area with uniform *S. subcrassa* growth and relatively homogeneous plant density, establishing 12 plots of 1 m × 1 m with 15–25 m buffer zones between them. The experiment included four precipitation treatments: W1 (20 mm added once monthly), W2 (10 mm added twice monthly), W4 (5 mm added four times monthly), and CK (natural precipitation). Rainfall simulations were performed from 19:30 to 21:30 using an automatic sprinkler (MZ911-ZKQ2-40) on predetermined dates. The sprinkler system mimicked agricultural spray irrigation, effectively preventing surface runoff and ensuring accurate precipitation addition. Based on multi-year data, natural rainfall primarily occurs from May to August, totaling 150–200 mm and accounting for most annual precipitation. As rainfall magnitude increases, event probability decreases and intervals between events increase. Specific application dates were: W1 on the 15th of each month; W2 on the 5th and 20th of each month; and W4 on the 5th, 10th, 15th, and 20th of each month. Each treatment had three replicates, with three long-term observation plants marked per plot.

1.4 Sample Collection and Measurement

We collected samples on May 15 (growth period), July 15 (fruit development period), and September 15 (seed maturation period) using the harvest method. In each plot, we randomly collected three *S. subcrassa* plants (excluding the three marked observation plants), separated them into leaves, stems, and fruits in the laboratory, and oven-dried them at 105°C for 30 minutes, then at 65°C to constant weight. Samples were ground in a ball mill and stored in a cool, dry place. All measurements were conducted at the Fukang Station laboratory. Carbon content was measured using the high-temperature external heating potassium dichromate volumetric method. Nitrogen content was determined by the Kjeldahl method. Phosphorus content was measured using the molybdenum-antimony anti-colorimetric method. NDF, ADF, and ADL contents were determined using a semi-automatic fiber analyzer (ANKOM Technology). We defined structural carbohydrates as the sum of cellulose, hemicellulose, and lignin (NDF + ADF + ADL), while non-structural substances comprised all non-structural carbohydrates.

1.5 Data Analysis

Figures were created using Origin 2018. One-way ANOVA, multi-factor ANOVA, and significance testing across treatments and growth periods were performed in SPSS 22.0. Multiple comparisons were conducted using Fisher' s method in Minitab, with significance level set at $\alpha = 0.05$. Data are presented as means ± standard error (n = 3).

2 Results

2.1 Effects of Rainfall Frequency on Stoichiometry, NDF, ADF, and ADL

Three-way ANOVA revealed that rainfall frequency significantly affected N content ($P < 0.05$) and highly significantly affected P, C:N, C:P, and N:P ratios ($P < 0.001$) (Table 1). Growth stage, organ type, and their interaction highly significantly affected all indicators ($P < 0.001$). Rainfall frequency highly significantly affected NDF content ($P < 0.001$) and significantly affected ADF content ($P < 0.05$). Growth stage only highly significantly affected NDF content ($P < 0.001$). The interaction between rainfall frequency and growth stage significantly affected N content ($P < 0.05$) and highly significantly affected NDF content ($P < 0.001$). The interaction between rainfall frequency and organ type significantly affected N content ($P < 0.05$) and highly significantly affected NDF and ADF contents ($P < 0.001$). The interaction between growth stage and organ type highly significantly affected all indicators ($P < 0.001$). The three-way interaction highly significantly affected NDF content ($P < 0.001$) and significantly affected N content ($P < 0.05$).

2.2 Effects of Rainfall Frequency on C, N, and P Contents in *S. subcrassa*

Carbon content in *S. subcrassa* organs was relatively stable across precipitation treatments, with minimal variation (Figure 2). Leaf, stem, and fruit C content ranged from 19.45%-27.26%, 25.90%-37.15%, and 27.05%-33.59%, respectively. Across all growth stages, organ C content generally followed the pattern: stems > fruits > leaves. Under each precipitation treatment, C content in leaves, stems, and fruits remained relatively stable, with slight increases observed in the W4 treatment.

Nitrogen content in leaves, stems, and fruits ranged from 0.50%-0.96%, 0.43%-0.72%, and 0.91%-1.32%, respectively. The W4 treatment significantly increased leaf N content during the flowering-fruiting and fruit development periods compared to CK ($P < 0.05$). Compared to other treatments, W4 significantly increased stem N content during the fruit development period ($P < 0.05$). Fruit N content ranged from 0.91%-1.32%; W4 significantly increased fruit N content during the fruit development period compared to CK ($P < 0.05$). Throughout the growth period, organ N content generally followed: fruits > leaves > stems. Leaf and stem N content decreased with plant growth, while fruit N content increased.

Phosphorus content in leaves, stems, and fruits ranged from 0.11%-0.15%, 0.05%-0.11%, and 0.05%-0.11%, respectively. W4 significantly increased leaf P content during the fruit development period compared to other treatments ($P < 0.05$). Stem P content ranged from 0.04%-0.07%; W4 significantly increased stem P content during the fruit development period compared to CK ($P < 0.05$). Fruit P content ranged from 0.05%-0.11%; W4 significantly increased fruit P content during the fruit development period compared to CK ($P < 0.05$). Throughout the growth stage, organ P content generally followed: fruits > leaves > stems. Leaf and stem P content decreased with plant growth, while fruit P content increased.

2.3 Effects of Rainfall Frequency on Stoichiometric Ratios in *S. subcrassa*

The C:N ratio in *S. subcrassa* leaves ranged from 21.50-36.90 (Figure 3). W4 treatment significantly decreased leaf C:N during the seed maturation period compared to CK ($P < 0.05$). Stem C:N ranged from 50.29-88.90; W4 significantly decreased stem C:N during the seed maturation period compared to other treatments ($P < 0.05$). Fruit C:N ranged from 17.92-36.90, with minimal variation across treatments. Throughout the growth period, organ C:N generally followed: stems > leaves > fruits. Leaf and stem C:N increased with plant growth, while fruit C:N showed little change.

The C:P ratio in leaves ranged from 192.9-538.6; leaf C:P during the growth period was significantly lower than other periods ($P < 0.05$). Treatments showed no significant effect on leaf C:P ($P > 0.05$). Stem C:P ranged from 295.6-901.0; W4 significantly decreased stem C:P during the flowering-fruiting period compared to other treatments ($P < 0.05$). Fruit C:P ranged from 307.0-457.6; W4 significantly decreased fruit C:P during the fruit development period compared to other treatments ($P < 0.05$). Throughout the growth period, organ C:P generally followed: stems > fruits > leaves. Leaf and stem C:P increased with plant growth, while fruit C:P decreased.

The N:P ratio in leaves ranged from 4.6-16.8; W4 significantly increased leaf N:P during the fruit development period compared to CK ($P < 0.05$). Stem N:P ranged from 9.8-18.5; treatments showed minimal effect ($P > 0.05$). Fruit N:P ranged from 7.2-16.6; W4 significantly increased fruit N:P during the fruit development period compared to CK ($P < 0.05$). Throughout the growth period, organ N:P showed little variation. Leaf and stem N:P increased with plant growth, while fruit N:P decreased.

2.4 Effects of Rainfall Frequency on NDF, ADF, ADL, and Non-structural Substances

As *S. subcrassa* grew, NDF content in leaves and stems increased under all precipitation treatments, while changing little in fruits (Figure 4). Content distribution followed: stems > fruits > leaves. Leaf NDF ranged from 9.08%-19.46%; W4 significantly increased leaf NDF during the fruit development period compared to other treatments ($P < 0.05$). Leaf NDF during the rapid growth period was significantly lower than other periods ($P < 0.05$). Stem NDF ranged from 41.43%-54.96%; W4 significantly decreased stem NDF during the fruit development period compared to other treatments ($P < 0.05$). Fruit NDF ranged from 30.12%-36.31%; W4 significantly increased fruit NDF during the fruit development period compared to CK ($P < 0.05$).

ADF content in leaves ranged from 2.46%-5.51%, with significant differences across periods ($P < 0.05$). W4 significantly decreased leaf ADF during the seed maturation period compared to other treatments ($P < 0.05$). Stem ADF ranged from 5.63%-8.59%; W4 significantly decreased stem ADF during the growth period compared to other treatments ($P < 0.05$). Compared to the latter two periods, leaf ADF during the rapid growth period was significantly lower ($P < 0.05$). Fruit ADF ranged from 2.45%-3.24%; W4 significantly increased fruit ADF during the fruit development period compared to other treatments ($P < 0.05$).

ADL content in leaves ranged from 0.15%-1.83%; leaf ADL during the rapid growth period was significantly lower than other periods ($P < 0.05$). W4 significantly decreased leaf ADL during the fruit development period compared to other treatments ($P < 0.05$). Stem ADL ranged from 5.51%-8.59%; W4 significantly decreased stem ADL during the fruit development period compared to other treatments ($P < 0.05$). Fruit ADL ranged from 2.46%-5.51%; W4 significantly decreased fruit ADL during the seed maturation period compared to other treatments ($P < 0.05$).

Non-structural substance content in leaves and stems decreased overall with plant growth, while changing little in fruits (Figure 5). Content distribution followed: leaves > fruits > stems. Leaf non-structural substances ranged from 23.54%-46.62%; content during the flowering-fruiting period was significantly higher than other periods ($P < 0.05$). W4 significantly decreased stem non-structural substances during the growth period compared to other treatments ($P < 0.05$). Compared to CK, other treatments significantly increased leaf non-structural substances during the seed maturation period ($P < 0.05$). W4 significantly increased stem non-structural substances during the flowering-fruiting period ($P < 0.05$) and fruit non-structural substances during the fruit development period ($P < 0.05$).

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3 Discussion

3.1 Effects of Rainfall Frequency on C, N, and P Contents in *S. subcrassa*

Water availability influences the absorption, transport, allocation, and storage of organic carbon, total nitrogen, and total phosphorus in plants, thereby altering organ nutrient content. This study found that C content in *S. subcrassa* organs changed little with increasing rainfall frequency, likely because C exhibits high stability in plant tissues and constitutes a large proportion of plant biomass, making differences difficult to detect. In contrast, N and P contents showed greater variation with precipitation frequency, as these functional elements are more responsive to environmental changes. Organ nutrient content varies due to different functional requirements. Under different rainfall frequencies, the pattern of leaf N content changes throughout the growth period in W4-treated plants differed from other treatments, with leaf N content peaking during the fruit development period. This suggests that rainfall frequency affects leaf cell division capacity, with high-frequency, low-intensity precipitation maximizing this capacity. During the growth period, leaves accumulated substantial N, increasing leaf area and promoting photosynthesis. As fruits matured, leaf N accumulation decreased while stem N increased, and N gradually translocated to fruits, reflecting nutrient migration among organs during development.

3.2 Effects of Rainfall Frequency on Stoichiometric Ratios in *S. subcrassa*

Growth rate theory is fundamental to ecological stoichiometry, emphasizing that organisms adjust internal stoichiometric ratios to adapt to environmental changes and varying growth rates. Thus, nutrient ratio changes can indicate which elements limit plant growth, development, or reproduction and reveal nutrient use efficiency. In this study, N:P ratios in leaves and stems increased over time across all precipitation treatments. Compared to other treatments, W4 significantly increased leaf and fruit N:P during the fruit development period ($P < 0.05$), suggesting that P limitation intensified as plants grew, while high-frequency, low-intensity precipitation exacerbated this P limitation tendency. Herbaceous plants undergo rapid leaf cell division during the growth period, requiring substantial proteins and nucleic acids and thus higher N content. In this study, leaf N:P was higher during the growth period and decreased over time, likely because rapid early growth increased N demand for protein and nucleic acid synthesis. As plants senesced, reduced water content, enzyme activity, and physiological processes like transpiration diminished nutrient absorption, transport, and assimilation. Precipitation increases and higher frequency may accelerate soil element mobility, enhance root absorption and transport to shoots, and strengthen cation exchange between plants and soil, improving nutrient utilization efficiency and causing asymmetric element allocation among organs. Compared to CK, W4 increased leaf and fruit N:P ratios, likely related to increased precipitation frequency.

3.3 Effects of Rainfall Frequency on NDF, ADF, ADL, and Non-structural Substances and Their Relationship with Stoichiometric Characteristics

Structural carbohydrates, composed of cellulose, hemicellulose, and lignin that strengthen plant mechanical tissues and cell walls, are essential for water transport and drought survival. Higher content facilitates water transport, enabling longer survival in arid environments. In *S. subcrassa*, NDF, ADF, and ADL content distribution followed: stems > fruits > leaves. This likely reflects the stem' s primary role in water and nutrient transport. N is essential not only for ribosomal protein synthesis but also for photosynthate accumulation and transport. Compared to other treatments, W4 significantly increased leaf NDF during the fruit development period ($P < 0.05$) while decreasing non-structural substance content, suggesting coupling between stoichiometric characteristics and carbohydrate status under high-frequency, low-intensity rainfall.

Differences among organs under varying rainfall frequencies were substantial. In leaves, treatments other than CK generally reduced NDF content throughout the growth period, possibly because excess water limited enzymes related to lignin biosynthesis, altering cell wall lignification. All treatments except CK significantly increased leaf non-structural substances during seed maturation ($P < 0.05$), likely because moderate rainfall increases enhanced photosynthetic rates, benefiting non-structural carbohydrate accumulation. In stems, W4 reduced NDF content while increasing non-structural substances during the flowering-fruiting period. The opposite changes in stem non-structural substances and NDF content suggest that when water-stressed, plants first inhibit growth, reducing NDF synthesis. In fruits, W4 significantly increased NDF content during fruit development ($P < 0.05$), while non-structural substance changes showed the opposite pattern, possibly because high-frequency, low-intensity precipitation promotes growth and accelerates cell extension.

4 Conclusion

Our preliminary investigation of stoichiometric characteristics in different organs of *Salsola subcrassa* throughout its life history under varying rainfall frequencies on the southeastern edge of the Gurbantunggut Desert revealed that, compared to CK, the W4 treatment significantly increased C, N, and P contents in certain periods, enhanced N:P ratios, and increased fruit NDF content. High-frequency, low-intensity rainfall favored *S. subcrassa* growth, while different developmental stages showed varying nutrient demands, likely causing differences in water use efficiency. This provides a reference for further studies on nutrient absorption and utilization by desert vegetation and its environmental adaptability under drought conditions.

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