Effects of Nitrogen Addition and Precipitation Change on Physiological Indicators of Reaumuria soongarica (Postprint)

Authors: Yang Jie, Lishan Shan

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Abstract

Using red sand seedlings as the experimental material, we determined the contents of proline (Pro), chlorophyll (Chl), superoxide dismutase (SOD), peroxidase (POD), and soluble protein (SP) in red sand seedling leaves under different precipitation [30% precipitation reduction (W-), natural precipitation (W), and 30% precipitation increase (W+)] and nitrogen addition [N0 (0 g · m-2 · a-1), N1 (4.6 g · m-2 · a-1), N2 (9.2 g · m-2 · a-1), N3 (13.8 g · m-2 · a-1)] conditions. The results showed: (1) Under natural precipitation (W) and 30% precipitation increase (W+) conditions, the proline and chlorophyll contents of red sand seedlings showed an increasing trend with increasing nitrogen application rate, indicating that when water conditions are suitable, water and nitrogen exert a coupling effect to promote the accumulation of proline and chlorophyll. (2) Under N0 (no nitrogen addition) and low nitrogen (N1) levels, POD activity under natural precipitation (W) was significantly lower than that under 30% precipitation reduction (W-), while the opposite was observed under medium nitrogen (N2) and high nitrogen (N3) levels. This indicates that under low nitrogen levels, increased precipitation inhibits the enhancement of POD activity, while medium and high nitrogen addition greatly alleviates this inhibitory effect and promotes POD activity enhancement, demonstrating a compensatory effect between nitrogen and water. (3) Under natural precipitation (W) conditions, soluble protein content first increased and then decreased with increasing nitrogen addition, whereas under 30% precipitation reduction (W-) conditions, nitrogen addition had no significant effect on soluble protein content. This suggests that under normal water conditions, appropriate nitrogen addition promotes protein transformation in plants, but when nitrogen application reaches a certain critical threshold, continued increase in nitrogen content inhibits soluble protein production, while under water deficit conditions, nitrogen addition has no significant effect on protein transformation.

Full Text

Abstract

Water and nitrogen are the key factors limiting the growth and development of desert plants. To predict the impact of climate change on desert vegetation growth in the future, understanding the effects of nitrogen and water on plant physiology is essential. We investigated the effects of nitrogen application and precipitation on *Reaumuria soongorica* seedlings. Proline (Pro), chlorophyll (Chl), superoxide dismutase (SOD), peroxidase (POD), and soluble protein (SP) contents in *R. soongorica* leaves were measured under different precipitation treatments [precipitation decreases 30% (W^{-}), natural precipitation (W), and precipitation increases 30% (W^{+})] and nitrogen applications [N0(0 $g \cdot m^{-1}$), N1 (4.6 $g \cdot m^{-1}$), N2 (9.2 $g \cdot m^{-1}$), N3 (13.8 $g \cdot m^{-1}$)]. Under natural precipitation (W) and precipitation increases 30% (W^{+}), proline and chlorophyll contents increased with increased nitrogen application. The coupling effect of water and nitrogen promoted the accumulation of proline and chlorophyll when the water condition was suitable. In the no nitrogen (N0) and low nitrogen (N1) treatments, POD activity under natural precipitation (W) was significantly lower than that under precipitation decreases 30% (W^{-}), while the opposite trend was observed in the medium nitrogen (N2) and high nitrogen (N3) treatments. The results showed that at low nitrogen levels, increased precipitation inhibited POD activity, while the addition of nitrogen mitigated the inhibition and promoted POD activity, demonstrating the compensation effects of nitrogen and water. Under natural precipitation (W) conditions, the soluble protein content first increased and then decreased as the nitrogen concentration increased, while the effect of nitrogen addition on soluble protein content was not significant under precipitation decreases 30% (W^{-}). These findings demonstrate that under normal water conditions, appropriate nitrogen addition could promote the transformation of plant protein up to a certain concentration threshold, then continuous nitrogen increases inhibit soluble protein production. Conversely, nitrogen application had no significant effect on soluble protein transformation under water deficits.

Keywords: precipitation change; nitrogen addition; physiological index; *Reaumuria soongorica*

Introduction

Since the mid-20th century, human activities such as fossil fuel combustion and chemical fertilizer use have increased dramatically [1], leading to a rapid rise in atmospheric nitrogen compound emissions. Global nitrogen deposition rates are projected to increase by 2-3 times by the end of the 21st century [2]. Studies have shown that moderate increases in exogenous nitrogen can alter plant physiological processes, stimulate plant growth, and enhance plant resistance [3-5]. However, some researchers have found that nitrogen addition can inhibit plant growth and make plants more sensitive to water stress changes [6-8]. Other studies have reported that nitrogen has significant positive regulatory effects on plants under no water stress, negligible effects under mild water stress, and negative effects under severe water stress [9-11]. Plant physiological indices provide a comprehensive reflection of plant growth status, and both water stress and nitrogen deposition affect internal physiological and biochemical indicators [12-14].

Water and nitrogen impacts on plants are interdependent [15]. Research indicates that nitrogen deposition can enhance plant drought resistance and alleviate the inhibitory effects of water stress on plant growth [16-18]. However, other studies have found that nitrogen addition inhibits plant growth and increases sensitivity to water stress [19-21]. Since the 21st century, global precipitation patterns have changed substantially due to climate change, with increased frequency of extreme weather and drought events [22]. Precipitation, as the most critical limiting factor for vegetation growth and development, profoundly influences plant physiological ecology [23]. The arid and semi-arid regions of northwestern China are extremely sensitive to global change, and precipitation and nitrogen concentration have become key factors restricting ecosystem restoration and plant growth in this region [24-26]. Therefore, strengthening research on the physiological responses of desert plants to precipitation change and nitrogen deposition is crucial for theoretically elucidating the physiological and ecological response mechanisms of desert plants to nitrogen and water changes, and for guiding vegetation protection, restoration, and reconstruction.

Reaumuria soongorica, also known as 琵琶柴, is a dominant and constructive species in desert shrub vegetation in the arid and semi-arid regions of northwestern China [27-29]. It possesses strong drought resistance, salt tolerance, and ecological adaptability [30-32], playing an important role in protecting and improving desert ecosystems. Current research on *R. soongorica* has primarily focused on biomass allocation [33], photosynthetic and fluorescence characteristics [34], and root morphology [35] under single-factor water stress. However, recent studies have shown that climate-related environmental factors affect ecosystem functions synergistically [36-38]. Research on multi-factor interactions has mainly focused on water stress and CO_2 concentration changes [39-41]. As nitrogen is a key factor limiting vegetation growth and distribution in arid and semi-arid ecosystems, studies on the combined effects of nitrogen and water on *R. soongorica* physiological indices are limited. Therefore, this study used *R. soongorica* seedlings as experimental material, controlling precipitation and nitrogen concentrations during the growing season to measure changes in leaf physiological indices, aiming to explore the mechanisms of nitrogen and water effects on *R. soongorica* physiology and provide theoretical guidance for predicting future climate change impacts on desert vegetation and for vegetation restoration.

Materials and Methods

1.1 Experimental Material Cultivation

In early May, *R. soongorica* seedlings with consistent growth (average height 10 cm) were selected from their natural distribution area. All seedlings were transplanted into pots (upper diameter 35 cm, height 26 cm) containing 13 kg of soil at the experimental base of Gansu Agricultural University. One seedling was planted per pot. The experiment included three precipitation gradients and four nitrogen levels, with five replicates per treatment, totaling 180 seedlings. After transplanting, seedlings were managed with daily watering and shading to ensure survival during the recovery period.

1.2 Experimental Design

The precipitation gradients were set according to the monthly average rainfall in the typical distribution area of *R. soongorica* during the growing season (May–September). Based on meteorological data from the China Meteorological Administration, the multi-year average natural rainfall in the distribution area was 142 mm. In high-rainfall years, precipitation was about 110 mm higher than the multi-year average, while in low-rainfall years, it was about 77 mm lower. This experiment simulated annual precipitation by decreasing 30% (110 mm), maintaining natural precipitation (142 mm), and increasing 30% (77 mm). The monthly precipitation distribution was calculated based on the proportion of monthly precipitation during the growing season [42], and then converted to irrigation amounts according to pot diameter.

Referring to atmospheric nitrogen deposition levels in northwestern desert regions [43], four nitrogen addition levels were established: control ($0\ g \cdot m^{-1}$), low nitrogen ($4.6\ g \cdot m^{-1}$), medium nitrogen ($9.2\ g \cdot m^{-1}$), and high nitrogen ($13.8\ g \cdot m^{-1}$). Urea [$CO(NH_2)_2$] was used as the nitrogen source. Based on the nitrogen content of urea (46.7%), the amounts applied per pot were calculated as 0 g, 0.8865 g, 1.7730 g, and 2.6595 g, respectively. These amounts were sprayed evenly onto the soil surface during the *R. soongorica* growing season from May to September.

1.3 Sample Collection and Index Determination

Sampling was conducted three times during the growing season (mid-July, mid-August, and early September), with five pots sampled each time. On clear days, healthy fresh leaves from the middle and upper parts of *R. soongorica* seedlings were collected in test tubes with lids, placed in an ice box, and immediately transported to the laboratory for physiological index determination.

1.4 Physiological Index Determination Methods

Proline content was measured using the sulfosalicylic acid extraction method [44]. Chlorophyll content was determined by the acetone colorimetric method

[45]. Superoxide dismutase (SOD) activity was assayed using the nitroblue tetrazolium (NBT) method [46]. Peroxidase (POD) activity was measured by the guaiacol method [47]. Soluble protein content was determined using the Coomassie brilliant blue G-250 method [48].

1.5 Data Processing and Analysis

SPSS 20.0 was used for statistical analysis. Two-way ANOVA was performed to analyze the effects of nitrogen addition and precipitation on *R. soongorica* physiological indices. One-way ANOVA was conducted for physiological indices under the same precipitation (or nitrogen addition) level with different nitrogen addition (or precipitation) levels, followed by LSD multiple comparisons. Figures were created using Excel 2016. All values are presented as mean ± standard error.

Results and Analysis

2.1 Chlorophyll Content Dynamics Under Different Precipitation and Nitrogen Treatments

Two-way ANOVA showed that nitrogen addition had extremely significant effects on chlorophyll content ($P < 0.001$) . Under natural precipitation (W), chlorophyll content in *R. soongorica* increased with nitrogen addition, reaching maximum values at high nitrogen levels. Under precipitation decrease 30% (W^-) and precipitation increase 30% (W^+), chlorophyll content first increased and then decreased with nitrogen addition, peaking at medium nitrogen levels [Figure 1: see original paper].

Under natural precipitation (W), chlorophyll content at the high nitrogen level increased by 34.42%, 32.58%, and 7.25% compared to no nitrogen, low nitrogen, and medium nitrogen treatments, respectively. Under precipitation increase 30% (W^+), chlorophyll content at medium nitrogen level increased by 70.81%, 55.26%, and 31.49% compared to no nitrogen, low nitrogen, and high nitrogen treatments, respectively. At each precipitation gradient, chlorophyll content in nitrogen-treated plants was significantly higher than in non-treated plants. Under each nitrogen level, chlorophyll content under precipitation increase 30% (W^+) was significantly higher than under precipitation decrease 30% (W^-) and natural precipitation (W).

2.2 Proline and Soluble Protein Content Dynamics

Two-way ANOVA indicated that nitrogen addition had extremely significant effects on proline content ($P < 0.01$) . Under natural precipitation (W), proline content increased with nitrogen addition, with the high nitrogen treatment showing 123.31%, 15.39%, and 7.36% higher proline content than no nitrogen, low nitrogen, and medium nitrogen treatments, respectively. Under precipitation decrease 30% (W^-), proline content decreased significantly with increasing nitrogen concentration. Under precipitation increase 30% (W^+), proline content increased with nitrogen addition, with values 54.50% and 20.03% higher than under natural precipitation at low and medium nitrogen levels, respectively [Figure 2: see original paper].

At each precipitation gradient, proline content in nitrogen-treated plants was significantly higher than in non-treated plants. Under different nitrogen levels, proline content under precipitation increase 30% (W^+) was significantly higher than under natural precipitation (W). At high nitrogen levels, proline content increased with precipitation amount.

Under natural precipitation (W) and precipitation increase 30% (W^+), soluble protein content in nitrogen-treated plants was higher than in non-treated plants. Under natural precipitation (W), soluble protein content first increased and then decreased with nitrogen addition, peaking at medium nitrogen levels with a 54.44% increase over no nitrogen. Under precipitation increase 30% (W^+), soluble protein content at low, medium, and high nitrogen levels increased by 98.89%, 49.32%, and 92.53% compared to no nitrogen, respectively. Under no nitrogen, soluble protein content decreased with increasing precipitation, while it increased under low nitrogen. The maximum soluble protein content occurred under the combination of medium nitrogen and natural precipitation.

2.3 SOD and POD Activity Dynamics

Under natural precipitation (W), SOD activity increased gradually with nitrogen addition, with high nitrogen levels showing 59.02%, 18.42%, and 12.32% higher activity than no nitrogen, low nitrogen, and medium nitrogen, respectively. Under precipitation decrease 30% (W^-), SOD activity decreased significantly with nitrogen addition, with no nitrogen treatment showing 28.15%, 27.56%, and 54.45% higher activity than low, medium, and high nitrogen treatments, respectively [Figure 3: see original paper].

At low nitrogen levels, SOD activity increased gradually with precipitation, with precipitation increase 30% (W^+) showing 11.89% and 44.26% higher activity than precipitation decrease 30% (W^-) and natural precipitation (W), respectively. At high nitrogen levels, SOD activity decreased with increasing precipitation, with precipitation increase 30% (W^+) showing 36.35% and 83.35% lower activity than natural precipitation and precipitation decrease 30% (W^-), respectively. The maximum SOD activity occurred at high nitrogen under precipitation decrease 30% (W^-), increasing by 1.16% and 16.34% compared to natural precipitation and precipitation increase 30% (W^+), respectively.

Under precipitation decrease 30% (W^-), POD activity increased with nitrogen addition, showing 19.78%, 52.11%, and 158.20% higher activity at no nitrogen compared to low, medium, and high nitrogen, respectively. Under each nitrogen level, POD activity under precipitation decrease 30% (W^-) was significantly lower than under natural precipitation (W). The maximum POD activity occurred at medium nitrogen under natural precipitation (W), increasing by 39.41% and 128.48% compared to low and high nitrogen, respectively. Under no nitrogen and low nitrogen, POD activity decreased significantly with increasing precipitation, with precipitation decrease 30% (W^-) showing 52.45% and 132.22% higher activity than natural precipitation (W), respectively. Under medium and high nitrogen, POD activity peaked under natural precipitation (W).

2.4 Correlation Analysis of Physiological Indices

Correlation analysis showed that under different precipitation and nitrogen treatments, physiological indices of *R. soongorica* were interrelated. Proline content was positively correlated with chlorophyll content ($P < 0.05$) and significantly positively correlated with soluble protein content ($P < 0.05$), but significantly negatively correlated with POD activity ($P < 0.05$) . Under precipitation increase 30% (W^+) and high nitrogen, proline content increased by 169.49% compared to the minimum value. Under precipitation increase 30% (W^+) and medium nitrogen, chlorophyll content increased by 86.47% compared to the minimum value. These results indicate that increased precipitation combined with high nitrogen addition synergistically promoted proline accumulation, while increased precipitation with medium nitrogen addition enhanced chlorophyll content. When water conditions were favorable, water and nitrogen coupling effects promoted plant growth, consistent with findings in *Panicum miliaceum* seedlings [49].

Discussion

Chlorophyll is crucial for photosynthesis, and its content directly affects organic matter accumulation and plant growth [50]. Proline is an important osmotic regulator that provides carbon and nitrogen sources for protein synthesis and maintains normal physiological metabolism [51]. This study found that under natural precipitation (W), chlorophyll content increased with nitrogen addition, demonstrating the positive relationship between nitrogen as a chlorophyll component and chloroplast formation, chlorophyll synthesis, and accumulation. Under no nitrogen, low nitrogen, and medium nitrogen treatments, proline content under precipitation increase 30% (W^+) was significantly higher than under natural precipitation (W), indicating that water stress promotes proline accumulation to reduce internal osmotic potential and enhance water absorption capacity [52].

Nitrogen is a basic component of plant proteins and amino acids [53]. Protein content changes significantly under drought stress, low nitrogen, or high nitrogen conditions [54], affecting normal cell metabolism and osmotic balance maintenance. This study found that under no nitrogen, soluble protein content increased with decreasing precipitation, consistent with previous research showing that *R. soongorica* soluble protein content increases as soil water content decreases [55]. This suggests that under water deficit, high soluble protein content maintains lower osmotic potential to improve drought resistance [56].

Under natural precipitation (W), soluble protein content first increased and then decreased with nitrogen addition, peaking at medium nitrogen levels, similar to findings in winter wheat [57]. Under precipitation decrease 30% (W^-), nitrogen addition had no significant effect on soluble protein content. These results demonstrate that under normal water conditions, appropriate nitrogen addition promotes protein transformation, but continuous nitrogen increases beyond a critical threshold inhibit soluble protein production, while nitrogen has no significant effect under water deficit.

SOD and POD are important protective enzymes that scavenge reactive oxygen species [58]. Studies show that SOD and POD activities increase under adverse environmental conditions to maintain metabolic balance [59-60]. Under water stress, SOD activity often increases [61]. This study found that at low nitrogen levels, SOD activity increased with decreasing precipitation, indicating that water stress promotes SOD activity at low nitrogen. However, at high nitrogen levels, SOD activity decreased with increasing precipitation, suggesting that under water deficit, reduced enzyme activity prevents excessive accumulation of catalyzed oxygen radicals, minimizing reactive oxygen damage to cell membranes [62]. POD activity increased significantly with nitrogen addition under precipitation decrease 30% (W^-), while nitrogen addition inhibited POD activity enhancement under water deficit. At low nitrogen levels, increased precipitation inhibited POD activity, while medium and high nitrogen addition alleviated this inhibition and promoted POD activity, demonstrating nitrogen-water compensation effects. This compensation may result from a complementary mechanism between nutrients and water, where deficiency in one factor can be offset by increased availability of the other to achieve similar ecological effects [63]. This is consistent with findings that appropriate nitrogen application can alleviate adverse effects of excessive water on *Populus euphratica* seedlings [64].

Conclusion

Under natural precipitation (W) and precipitation increase 30% (W^+), chlorophyll and proline contents in *R. soongorica* increased with nitrogen addition, indicating that under favorable water conditions, water-nitrogen coupling effects promote proline and chlorophyll accumulation. Under normal water conditions, appropriate nitrogen addition promoted protein transformation, but continuous nitrogen increases beyond a critical threshold inhibited soluble protein production. Under water deficit, increased nitrogen addition inhibited SOD activity enhancement. Additionally, at low nitrogen levels, increased precipitation inhibited POD activity, while medium and high nitrogen addition alleviated this inhibition and promoted POD activity, demonstrating nitrogen-water compensation effects.

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