Effects of Simulated Precipitation and Nitrogen Deposition on the Photosynthetic Physiology of Haloxylon ammodendron on the Southern Edge of the Junggar Basin (Postprint)

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Abstract

Nitrogen deposition and precipitation pattern change are currently hot research topics against the background of global climate change, and also represent the two main limiting factors in desert ecosystems. Therefore, investigating their effects on desert plants facilitates a deeper understanding of desert ecosystem responses to global change. This study selected Haloxylon ammodendron, a constructive species in desert areas on the southern margin of the Junggar Basin, as the research subject, and established two water conditions (natural precipitation, W0; 30% increased precipitation, W1) and three nitrogen application levels (natural nitrogen deposition, N0; nitrogen addition of 30 kg(N) • hm−2 • a−1, N1; nitrogen addition of 60 kg(N) • hm−2 • a−1, N2), with continuous treatment for 2 years, to explore the effects of precipitation, nitrogen deposition and their interaction on diurnal photosynthetic variation and physiological-ecological characteristics of H. ammodendron. The results showed that precipitation, nitrogen deposition and their interaction had highly significant positive effects on the diurnal variation of net photosynthetic rate (Pn) of H. ammodendron; concurrently, based on the changing trends of Pn, intercellular CO2 concentration (Ci) and stomatal limitation value (Ls) of H. ammodendron, it was inferred that the photosynthetic "midday depression" of H. ammodendron was mainly caused by non-stomatal factors. Moreover, under W0 conditions, the malondialdehyde (MDA) content, antioxidant enzyme (POD, CAT, SOD) activities, soluble protein (Pr) and soluble sugar (SS) contents of H. ammodendron all decreased significantly with increasing nitrogen application, whereas the proline (Pro) content showed a trend of first decreasing then increasing; under W1 conditions, the MDA content, antioxidant enzyme (POD, CAT, SOD) activities and osmotic adjustment substance (Pro, Pr, SS) contents of H. ammodendron all showed a significant trend of first increasing then decreasing with increasing nitrogen application. Under both water conditions, except that the Pro content of H. ammodendron under W1N1 treatment was higher than that of the control group, all other treatments were significantly lower than the control group; simultaneously, the MDA content, antioxidant enzyme activities, Pr and SS contents of H. ammodendron were also significantly lower than those of the control group. Comprehensive analysis indicated that precipitation, nitrogen addition and their interaction were all beneficial to the growth of H. ammodendron, but the magnitude of their interaction effect depended on the ratio between the two.

Full Text

Preamble

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Abstract: Nitrogen deposition and altered precipitation patterns are critical research topics under global climate change and represent two primary limiting factors in desert ecosystems. Investigating their effects on desert plants enhances understanding of how these ecosystems respond to global change. This study examined *Haloxylon ammodendron*, a dominant species in desert regions along the southern margin of the Junggar Basin. Two water conditions [natural precipitation (W0) and 30% increased precipitation (W1)] and three nitrogen deposition levels [natural nitrogen deposition (N0), 30 kg(N) · hm^{-2} (N1), and 60 kg(N) · hm^{-2} (N2)] were established, with treatments applied continuously for two years to explore the impacts of precipitation, nitrogen deposition, and their interactions on diurnal photosynthetic patterns and physiological-ecological characteristics of *H. ammodendron*. Results showed that precipitation, nitrogen deposition, and their interactions exerted highly significant positive effects on diurnal variation of net photosynthetic rate (Pn). Based on concurrent changes in Pn, intercellular CO$_2$ concentration (Ci), and stomatal limitation (Ls), the photosynthetic "midday depression" in *H. ammodendron* was primarily attributed to non-stomatal factors. Under W0 conditions, malondialdehyde (MDA) content, antioxidant enzyme activities (POD, CAT, SOD), and soluble protein (Pr) and soluble sugar (SS) contents all decreased significantly with increasing nitrogen, while proline (Pro) content initially decreased then increased. Under W1 conditions, MDA content, antioxidant enzyme activities, and osmotic adjustment substances (Pro, Pr, SS) all showed significant initial increases followed by decreases with rising nitrogen levels. Across both water conditions, all treatments significantly reduced Pro, MDA, antioxidant enzyme activities, Pr, and SS contents compared to the control, except for Pro content under W1N1 which exceeded the control. Comprehensive analysis indicated that precipitation, nitrogen addition, and their interactions all benefited *H. ammodendron* growth, though the strength of interactive effects depended on the ratio between water and nitrogen.

Keywords: *Haloxylon ammodendron*; precipitation; nitrogen deposition; water-nitrogen interaction; photosynthetic physiological characteristics; southern margin of Junggar Basin

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1.1 Study Area Description

The study was conducted at the Fukang Desert Ecological Research Station (87°45 E, 44°30 N, 436 m elevation) of the Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, located in Fukang County, Xinjiang, at the northern foothills of the Tianshan Mountains and southern margin of the Junggar Basin. The region has a temperate continental arid desert climate with a mean annual temperature of 6.1 °C (maximum 41.1 °C, minimum -34.4 °C), mean annual precipitation of 117.2 mm, and mean annual evaporation of 1,942.1 mm. Vegetation consists of typical desert shrubs, semi-shrubs, and semi-arboreal species growing sparsely either singly or in mixed stands, with *Haloxylon ammodendron* being one of the dominant windbreak and sand-fixation species.

1.2 Experimental Design

The experiment began in early 2014 within a fenced sandy plot at the research station. The *H. ammodendron* plantation had an average density of 600 plants $\cdot$ hm^{-2}, canopy closure of 0.5–0.7, and mean plant height of 180 cm. A flat area with relatively uniform *H. ammodendron* distribution and consistent tree age and growth status was selected as the experimental site. Within this area, 10 m × 10 m plots were established, with each plot containing at least seven *H. ammodendron* individuals. Four replicates were established for each treatment: control (W0N0), precipitation treatment (W1N0), nitrogen deposition treatments (W0N1 and W0N2), and water-nitrogen interaction treatments (W1N1 and W1N2).

Precipitation treatments comprised natural precipitation (W0) and 30% increased precipitation (W1). The 30% increase was calculated based on the

30-year average annual precipitation of 200 mm in Fukang, totaling an additional 60 mm. This supplemental precipitation was distributed equally across spring, summer, and autumn seasons (20 mm per season). Spring supplementation began on March 25, summer on June 20, and autumn on August 20, applied weekly at 5 mm per event for four weeks, between 6:00–8:00 AM. To ensure accurate delivery and better simulate natural precipitation, water was transported to the site one day prior, stored in dedicated tanks, and applied using a sprinkler irrigation system.

Nitrogen deposition treatments included natural deposition (N0), 30 $kg(N) \cdot hm^{-2}$ (N1), and 60 $kg(N) \cdot hm^{-2}$ (N2) above natural levels. Increased nitrogen was applied as ammonium nitrate (NH_4NO_3), the dominant form of nitrogen deposition in the region. To facilitate plant uptake and simulate natural deposition, NH_4NO_3 was dissolved in 100 L water and sprayed uniformly into plots using a sprayer to minimize nutrient loss. Control plots received equal amounts of water without nitrogen. Applications were conducted in spring, summer, and autumn on the same dates as precipitation treatments.

1.3 Gas Exchange Parameter Measurements

Gas exchange parameters were measured during the peak growing season (July 2015) on clear days using a portable photosynthesis system (Li-6400XT, LI-COR, USA). Healthy *H. ammodendron* plants were randomly selected from each plot, with three clusters of assimilating branches (three replicates) per plant measured at similar positions, yielding 15 datasets per treatment that were averaged for statistical analysis. Measurements were taken from 8:00 to 20:00 at 2-hour intervals. Parameters automatically recorded by the system included net photosynthetic rate (Pn) and intercellular CO_2 concentration (Ci). Instantaneous water use efficiency (WUE) and stomatal limitation (Ls) were calculated as: $WUE = Pn/Tr$ (where Tr is transpiration rate) and $Ls = 1-Ci/Ca$ (where Ca is atmospheric CO_2 concentration) [14,15]. Soil samples were collected from each plot at 60 cm depth using an auger, placed in aluminum boxes, and transported to the laboratory for physicochemical analysis.

1.4 Plant Material and Physiological Index Measurements

Following gas exchange measurements, tender tips of *H. ammodendron* assimilating branches were collected in centrifuge tubes, immediately stored in liquid nitrogen, and transported to the laboratory for analysis of: malondialdehyde (MDA) content, peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD) activities, and proline (Pro), soluble protein (Pr), and soluble sugar (SS) contents. MDA was determined by the thiobarbituric acid method, POD by the guaiacol method, CAT by the iodometric method, SOD by the nitroblue tetrazolium (NBT) photochemical reduction method [16], Pro by the sulfosalicylic acid method, Pr by the Coomassie brilliant blue method, and SS by the anthrone colorimetric method [17]. Optical density was measured using a G-250 spectrophotometer. Four replicates were measured per treatment and averaged for statistical analysis.

1.5 Data Analysis

Two-way ANOVA was used to analyze treatment effects on soil physicochemical characteristics [soil water content (WCS), electrical conductivity (EC), pH, organic matter (SOM), total nitrogen (TN), total phosphorus (TP), total potassium (TK)] and plant physiological indices (MDA, POD, SOD, CAT, Pro, Pr, SS). One-way ANOVA was used to compare these indices and gas exchange parameters (Pn, Ci, Ls, WUE) among treatments, with LSD (Least Significant Difference) tests for multiple comparisons ($P < 0.01$ and $P < 0.05$). Statistical analyses were performed using SPSS 17.0, and figures were generated using Origin 8.0.

2.1 Response of Soil Physicochemical Properties to Precipitation and Nitrogen Addition

Two-way ANOVA revealed that nitrogen and water treatments significantly affected WCS, EC, SOM, TN, and TK contents, significantly influenced soil pH, while precipitation alone did not significantly affect TP content (Table 1).

Under W0 conditions, WCS, EC, SOM, TN, and TP contents increased significantly with nitrogen addition, while pH and TK showed initial increases followed by decreases. All treatment differences were highly significant except for pH between N0 and N2. Under W1 conditions, SOM, TN, and TP increased significantly with nitrogen addition, while WCS and EC showed initial increases then decreases with highly significant inter-group differences. TK exhibited the same pattern as under W0 conditions (Table 2).

2.2 Response of Gas Exchange Parameters to Different Treatments

ANOVA indicated that nitrogen and precipitation treatments significantly affected assimilating branch gas exchange. Under W0 conditions, Pn at 8:00, 18:00, and 20:00 showed significant initial increases then decreases with nitrogen addition, while at other times (except 14:00 for N0 vs. N1) Pn increased significantly with nitrogen. Under W1 conditions, Pn at 8:00 and 20:00 followed the same pattern as W0, while at other times showed significant initial decreases then increases. All treatments exhibited typical "bimodal" diurnal Pn patterns with consistent peak and trough timing (Figure 1a [Figure 1: see original paper]).

Leaf Ci, influenced by multiple environmental and internal factors, ultimately affects photosynthesis. Under W0 conditions, Ci (except at 12:00) decreased significantly with nitrogen addition, showing a bimodal diurnal pattern with peaks at 8:00 and 16:00 and a trough at 10:00. Under W1 conditions, Ci at 8:00

and 20:00 showed initial decreases then increases, while at other times showed initial increases then decreases, maintaining a bimodal pattern with peaks and troughs consistent with W0 conditions (Figure 1b [Figure 1: see original paper]).

Stomatal limitation (Ls) reflects reduced CO_2 entry due to decreased stomatal conductance. Statistical analysis revealed significant diurnal variation in Ls among treatments. Under W0 conditions, Ls (except at 12:00) increased significantly with nitrogen addition. Under W1 conditions, Ls at 8:00 decreased with nitrogen addition, while at 20:00 showed initial increases then decreases, with opposite trends at other times. All treatments showed bimodal Ls patterns, with the first peak at 10:00 and the second peak at 18:00 (for W0N0, W1N0, W1N2) or 20:00 (other treatments). Troughs occurred at 14:00 and 16:00 under the two water conditions (Figure 1c [Figure 1: see original paper]).

Water use efficiency (WUE) reflects the relationship between water consumption and dry matter production, serving as a comprehensive indicator of plant growth suitability. Except at 14:00, WUE showed consistent trends with increasing nitrogen across water conditions, with all treatments displaying clear bimodal diurnal patterns. The first peak occurred at 10:00 (except W0N1 at 8:00), troughs at 14:00, and second peaks at 18:00 (Figure 1d [Figure 1: see original paper]).

2.3 Response of MDA Content, Antioxidant Enzyme Activities, and Osmotic Adjustment Substances

Two-way ANOVA showed that nitrogen and precipitation treatments significantly affected MDA, Pro, Pr, and SS contents and POD, SOD, and CAT activities (Table 3).

MDA serves as a key indicator of plant cell damage under stress. Under W0 conditions, MDA content decreased significantly with nitrogen addition. Under W1 conditions, MDA showed significant initial increases then decreases, but remained significantly higher than N0 levels (2.3-fold and 1.4-fold higher, respectively). All treatments significantly reduced MDA compared to the control (Figure 2a [Figure 2: see original paper]).

In the antioxidant enzyme system, POD and SOD are crucial protective enzymes that scavenge reactive oxygen species, with POD defending against membrane lipid peroxidation and SOD clearing potential hydrogen peroxide damage. CAT also plays vital roles in maintaining cellular oxidative metabolism, water balance, and photosynthesis. Under both W0 and W1 conditions, POD, CAT, and SOD activities showed consistent trends: decreasing significantly with nitrogen addition under W0, but showing initial increases then decreases under W1. All treatments reduced enzyme activities compared to the control (Figure 2b, 2c, 2d).

Osmotic adjustment represents another important physiological mechanism against stress, with proline, soluble protein, and soluble sugar being key osmotic regulators. Under W0 conditions, proline content showed significant initial decreases then increases with nitrogen addition, but remained significantly lower than N0 levels. Under W1 conditions, proline showed significant initial increases then decreases, with N2 levels reaching 1.4 times the control value (Figure 2e). Soluble protein and soluble sugar contents decreased significantly with nitrogen addition under W0 conditions, while under W1 conditions they showed initial increases then decreases, with W1N1 levels significantly higher than W1N2 but lower than the control (Figure 2f, 2g).

Discussion

Soil physicochemical properties reflect soil structure, nutrient status, and water-holding capacity, forming essential factors influencing plant growth and biomass that are affected by vegetation type, soil formation mechanisms, ecosystems, and human activities [19]. Nitrogen deposition and precipitation pattern changes, as primary features of global climate change, directly affect soil moisture, pH, electrical conductivity, and nutrient status, with varying results across different treatments [20]. Under dry W0 conditions, soil WCS, EC, SOM, TN, and TP increased significantly with nitrogen addition, while pH and TK showed initial increases then decreases. This indicates that under drought stress, nitrogen addition improves soil water retention and rhizosphere nutrition, promoting plant growth and potassium absorption at certain nitrogen levels [21], likely related to plant growth status and nitrogen-potassium interactions [22]. Excessive nitrogen application can reduce soil pH [23]. Under moist W1 conditions, SOM, TN, TP, and TK showed similar trends, but other soil properties differed markedly: WCS and EC showed initial increases then decreases, while pH increased significantly with nitrogen addition, possibly because precipitation disrupted the original nutrient balance while increased nitrogen enhanced microbial activity, accelerating transformation of inorganic elements and organic matter formation [24].

Plant leaves are primary photosynthetic organs and sensitive indicators of environmental change [1], with physiological and biochemical characteristics reflecting both environmental impacts and plant adaptation [25]. Water and nitrogen are crucial environmental factors for plant growth and important components of biomass formation [20], so their variation inevitably affects plants. Numerous studies [26] demonstrate that precipitation and nitrogen addition significantly increase plant Pn, with interactive effects depending on their ratio. In this study, all treatments showed typical bimodal diurnal Pn patterns (“midday depression”). Based on the criterion that reduced Pn accompanied by decreased Ci and increased Ls indicates stomatal limitation, while the opposite indicates non-stomatal limitation, we confirmed that *H. ammodendron*’ s midday depression was primarily caused by non-stomatal factors, differing from Tian et al. [27]. Liu et al. [28] found nitrogen addition improved water use efficiency in spring wheat, while Wang et al. [29] reported WUE in cotton initially increased then decreased with irrigation and nitrogen addition. Our study confirmed both findings and further showed that *H. ammodendron* WUE initially decreased then increased with nitrogen addition, likely due to atmospheric temperature differences affecting soil evaporation. This supports the conclusion that nitrogen addition can compensate for water deficit stress under drought conditions, similar to findings in jujube [30], and demonstrates differential effects of water-nitrogen treatments on WUE, consistent with Li et al. [31].

Under normal conditions, reactive oxygen species production and scavenging maintain dynamic equilibrium [32], with stress disrupting this balance and causing membrane lipid peroxidation. MDA, the end product of oxidation, indicates membrane damage severity [33]. Under drought W0 conditions, MDA decreased with nitrogen addition, while under moist W1 conditions it showed initial increases then decreases. This suggests both precipitation and nitrogen addition alleviate water deficit damage, but interactive effects depend on specific ratios. Plants enhance protective enzyme activities to scavenge excess reactive oxygen species and reduce cellular damage. Studies show appropriate nitrogen addition significantly reduces POD, CAT, and SOD activities and MDA content under stress [34], while excessive nitrogen exacerbates membrane oxidation and reduces reactive oxygen scavenging capacity [34]. In this study, POD, CAT, and SOD activities mirrored MDA trends: decreasing with nitrogen addition under W0, but showing initial increases then decreases under W1, differing from Li et al. [35], possibly due to species-specific or condition-specific responses of protective enzymes to stress.

Proline and soluble sugars are major osmotic adjustment substances, with content changes related to stress resistance [36]. Soluble proteins, mostly enzyme proteins, are considered related to metabolic levels [37], though increased content also enhances stress resistance and adaptability [38]. Yang et al. [39] found proline content in *Aquilaria sinensis* seedlings increased significantly with nitrogen addition under water stress, differing from our results, likely due to species-specific response mechanisms. Wang et al. [38] reported soluble sugar and protein contents in *Zanthoxylum bungeanum* initially increased then decreased with soil moisture, and increased with fertilization. In contrast, *H. ammodendron* showed significant decreases in soluble sugar and protein with nitrogen addition under W0, but initial increases then decreases under W1, differing from Wang et al. [38], possibly because soluble sugars serve both as osmotic regulators and photosynthetic products [38], while soluble proteins are affected by plant metabolic levels under stress.

Conclusion

Precipitation and nitrogen addition significantly affected soil physicochemical properties, nutrient status, and photosynthetic physiology of *H. ammodendron*. Under drought conditions, nitrogen addition significantly improved rhizosphere nutrition and alleviated drought effects, while increasing protective enzyme activities (POD, CAT, SOD) and osmotic adjustment substances (Pro, SS, Pr), maintaining relatively low MDA levels and promoting photosynthetic rate and water use efficiency. Under moist conditions, nitrogen effects on stress resistance depended on the water-nitrogen interaction ratio. In this study, nitrogen additions of 30 kg(N) • hm^{-2} and 60 kg(N) • hm^{-2} both enhanced stress resistance more than natural nitrogen deposition, suggesting that increased precipitation and nitrogen deposition under future climate change scenarios will benefit *H. ammodendron* growth in the southern Junggar Basin region.

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