Study on the Effects of Different Non-growing Season Precipitation Treatments on the Photosynthetic Characteristics of Three Dominant Species in the desert steppes of Inner Mongolia

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Abstract. Climate change has altered the precipitation patterns of temperate grasslands. However, our understanding of the ecological effects of non-growing season precipitation changes remains limited. To explore the impact of non-growing season precipitation on the photosynthesis of typical desert grassland plants, this study focused on the desert grassland of Inner Mongolia. Four simulated water control treatments were set up for the non-growing season: 0 mm (CK), 10 mm (P1), 20 mm (P2), and water exclusion (P3). A four-year field precipitation control experiment was conducted. In the fourth year of the experiment, during the growing season, photosynthetic observations were conducted on dominant species under different precipitation treatments to investigate how non-growing season precipitation affects plant photosynthetic characteristics. The results showed that:

Among the three dominant species, *Stipa krylovii* exhibited the highest light saturation point, making it well-adapted to high-light intensity habitats in desert grasslands. *Leymus chinensis* and *Convolvulus ammannii* demonstrated higher light energy use efficiency under low light conditions, with higher apparent quantum efficiency and lower light compensation points. Moreover, their dark respiration rates were lower than that of *Stipa krylovii*, suggesting that they consumed fewer photosynthetic products through respiration and thus accumulated more organic matter. Comparing the light response curve parameters of *Convolvulus ammannii* under different precipitation treatments, it was found that *Convolvulus ammannii* was highly sensitive to the 20 mm (P2) water addition treatment, showing a stronger photosynthetic potential.

Analyzing the instantaneous photosynthetic parameters of the three dominant species revealed that *Stipa krylovii* exhibited increased net photosynthetic rate and water use efficiency under the 20 mm water addition condition, im-

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proving its photosynthetic efficiency. *Convolvulus ammannii*, under the 20 mm (P2) treatment, showed increases in net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO2 concentration, indicating that the increased water supply (P2) during the non-growing season also enhanced the photosynthetic capacity of *Convolvulus ammannii*.

Keywords: Non-growing season precipitation; Desert steppes; Light response curves; Water use efficiency

1 Introduction

Influenced by climate change, the hydrological cycle in watersheds has intensified, with a distinct trend of warming and wetting in mid- and high-latitude regions, including desert steppess [1, 2]. Compared to the growing season, the warming signal during the non-growing season is even more pronounced [3-5]. Sun Jianqi et al. [6] (2013) studied the response of winter precipitation and extreme precipitation to warming over the past 50 years in China on a decadal scale, finding that as winter temperatures in China increased, both winter precipitation and extreme precipitation showed a consistent upward trend, with the increase in extreme precipitation being significantly greater than that in non-extreme precipitation. Song et al. [7] (2019), while conducting an ecosystem water balance analysis during dry and wet years in the Xilamulun desert steppes, found that the water balance for plants was negative during the growing season, with the water deficit mainly sourced from non-growing season precipitation. This research reveals the ecological effects of changes in non-growing season precipitation patterns, which are crucial for assessing the impacts of climate change.

The Inner Mongolia desert steppes, located in the arid and semi-arid region, accounts for 8.1% of China's total grassland area and serves as an important ecological safety barrier in northern China [8]. As a transitional zone from grassland to desert, the region's ecological environment is particularly fragile and highly susceptible to climate change [9]. Photosynthesis, a key biological process in the carbon cycle of terrestrial ecosystems, is a hot topic in plant physiological ecology research [10]. Even subtle changes in photosynthetic processes can significantly affect the carbon balance of grassland ecosystems [11]. The light response curve, which describes the relationship between photosynthetic rate and light intensity, is an essential tool for understanding the mechanisms behind plant water-carbon interactions [12].

To investigate the mechanisms by which changes in non-growing season precipitation patterns affect the photosynthesis of drought-resistant plants, this study conducted a four-year non-growing season water control experiment in the Inner Mongolia desert steppes. We measured the light response curves and instantaneous photosynthetic parameters of three dominant species. The aim was to explore how different non-growing season precipitation treatments influence the leaf-scale photosynthetic physiological characteristics of the three dominant species in the desert steppes. The findings of this study will enhance our understanding of the adaptive mechanisms of desert steppes plants to climate change and provide scientific data for climate change impact assessments.

2 Materials and Methods

2.1 Study Area Overview

The research site is located at the Yinshan National Station for Ecological Hydrology, a field research facility affiliated with the China Institute of Water Resources and Hydropower Research, situated on the northern foothills of the Yinshan Mountains in Inner Mongolia (111°12'E, 41°24'N) (hereafter referred to as the "Yinshan National Station") (Figure 1). The long-term average annual precipitation at the station is 282.4 mm, and the long-term average annual evaporation is 2305.0 mm (E601). The soil type is calcic brown soil, with the dominant species being *Stipa krylovii*. Other dominant and companion species include Convolvulus ammannii, Leymus chinensis, *Cleistogenes squarrosa, Agropyron cristatum*, and *Artemisia frigida*. The natural vegetation has shallow roots, typically extending to a depth of 40 cm.

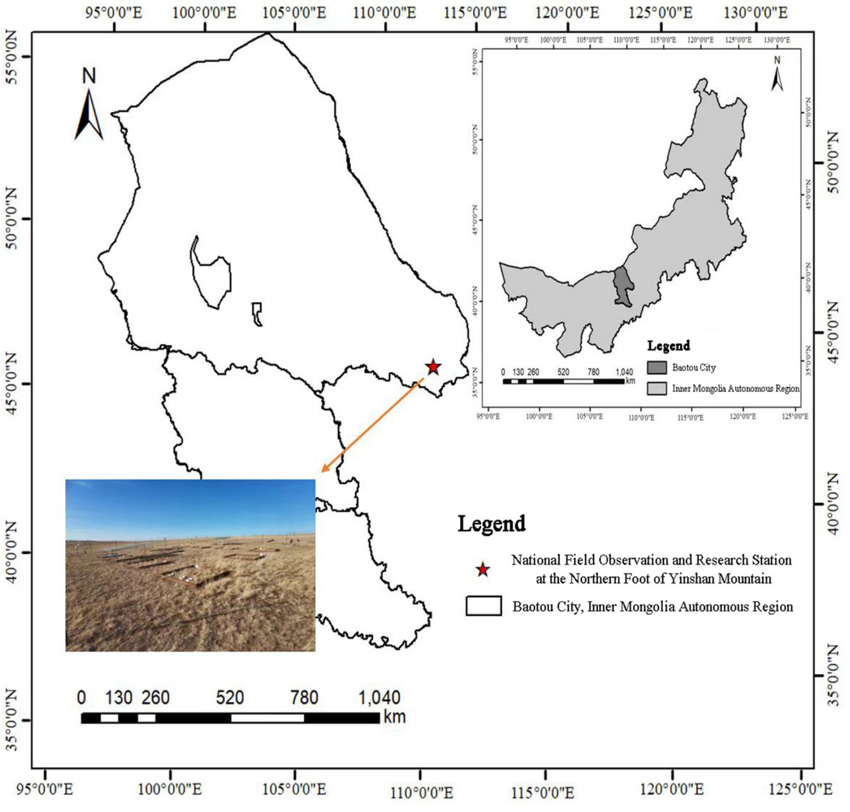

Fig. 1. Geographic Location of the Study Area

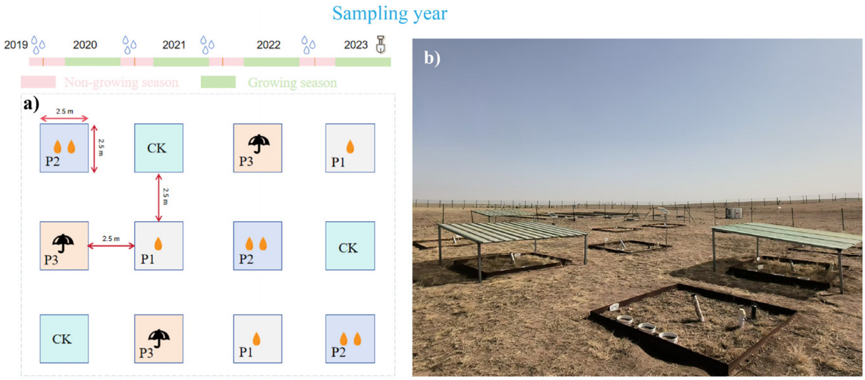

Fig. 2. Artificial Precipitation Experiment Site

2.2 Experimental Design

In 2019, based on the survey of the study plots, a natural grassland dominated by *Stipa* krylovii was selected, and 12 isolation plots (2.5 m × 2.5 m) were established for the artificial precipitation experiment (Figure 2b). From 2019 to 2022, precipitation control experiments were conducted during the non-growing season for four consecutive years.

Considering the global trend of increasing precipitation and the frequency of extreme precipitation events in high-latitude grasslands, we set up two precipitation increase treatments (high soil moisture conditions) and one water exclusion treatment (low soil moisture conditions). Based on historical local precipitation data and national precipitation grading standards (GB/T 28592-2012), the water addition treatments increased the natural precipitation by 20 mm (equivalent to a heavy rain or snowfall) and 10 mm (equivalent to moderate rain or snow). Additionally, to simulate extreme drought conditions during the non-growing season, a water exclusion treatment was set up using transparent shelters to block natural precipitation throughout the non-growing season while ensuring free ventilation. A control group was also set up for comparative analysis between the treatments. The treatments were randomly distributed across the plots, with three replicates per treatment, as detailed in Figure 2a.

Note: Experimental design and study location: a) Schematic of the isolated plots, b) Field location. In a), light blue and gray grids represent the precipitation increase of 20 mm and 10 mm during the non-growing season, respectively, while the orange grids with umbrellas represent the water exclusion treatment. The grid labeled "CK" represents the control plots.

2.3 Methodology

2.3.1 Light Response Curve Measurement.

The photosynthetic-light response curve was measured using a LI-6800 portable photosynthesis system (USA, LI-COR) in August 2023. For each treatment, three healthy plants of *Stipa krylovii*, *Leymus chinensis*, and *Convolvulus ammannii* were selected and measurements were conducted between 9:00 AM and 11:30 AM on sunny, windless days. The light intensity gradient was set as follows: 2000, 1800, 1600, 1400, 1200, 1000, 800, 400, 300, 200, 150, 100, 50, 20 μmol m^{-2} s^{-1}, with a data collection period of 120-300 seconds after each change in light intensity. The gas flow rate was set to 500 μmol/s, the CO_2 concentration in the leaf chamber was maintained at 400 μmol/mol, and the relative humidity was controlled around 60%, with a temperature setting of 25°C.

The light response curves were fitted using the rectangular hyperbola model [13] with the following equation:

$$Pn = aI\frac{1-\beta I}{1+\gamma I} - R_d$$

Where I is the light quantum flux density (μmol m-2 s-1), α is the initial quantum efficiency (μmol umol-1), i.e., the slope of the light-response curve at I=0, Pnmax is the maximum net photosynthetic rate (μmol m-2 s-1), Rd is the rate of dark respiration (μmol-m-2 s-1), β denotes the photoinhibitory term, and γ denotes the light saturation term.

Photosynthetic-light response curve fitting was conducted using the "Leaf Floating" photosynthesis software (version 4.1.1). The rectangular hyperbola model was selected because it can fit light response curves for plants across different habitats and directly estimate plant light saturation points and maximum net photosynthetic rates, distinguishing it from other models [13].

2.3.2. Determination of leaf gas Exchange Parameters.

In June-August 2023, mature and healthy plants were selected from each plot, and the photosynthetic physiology and other parameters of the three dominant plants were measured in situ using the LI-6800 Portable Photosynthesis Tester (LI-COR, USA) at a CO_2 concentration of 400 μmol/mol with a natural light source, and the average value was calculated as the final result for three plants of each type at the same leaf position, including: net photosynthetic rate (Pn, μmol m^{-2} s^{-1}), transpiration rate (Tr, mol m^{-2} s^{-1}), intercellular carbon dioxide concentration (Ci, μmol mol^{-1}), stomatal conductance (Gs, mol m^{-2} s^{-1}). $^{-2}$ s^{-1}), water use efficiency (WUE, μmol/mmol) was calculated as follows:

$$WUE = Pn / Tr$$

3 Results

3.1 Response of Photosynthetic Characteristics and Parameters of Plants to Moisture Changes Before Freeze-Thaw Period

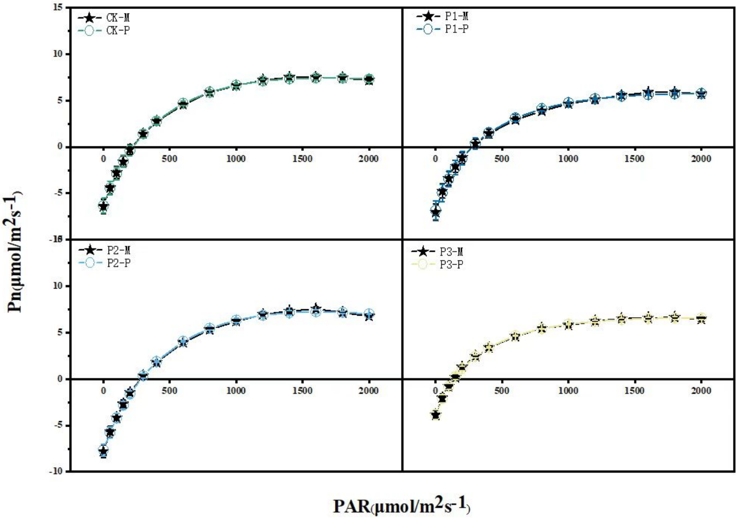

Fig. 3. Stipa *kryloyii* optical response curve of different moisture treatments

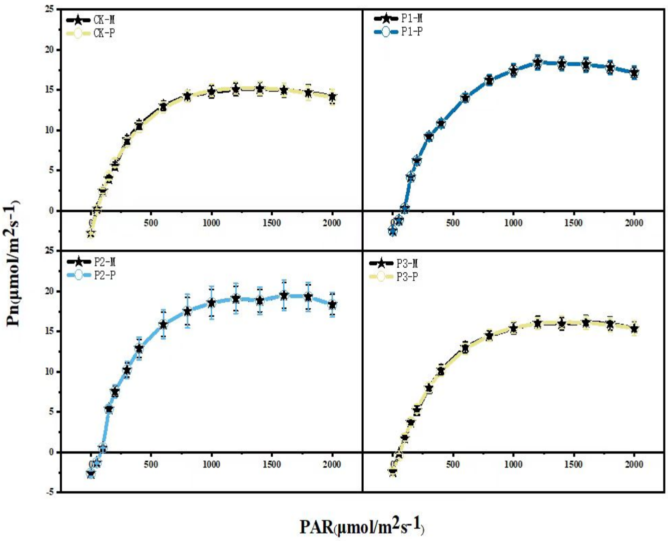

Fig. 4. Light response curves of *Leymus chinensis* with different moisture treatments

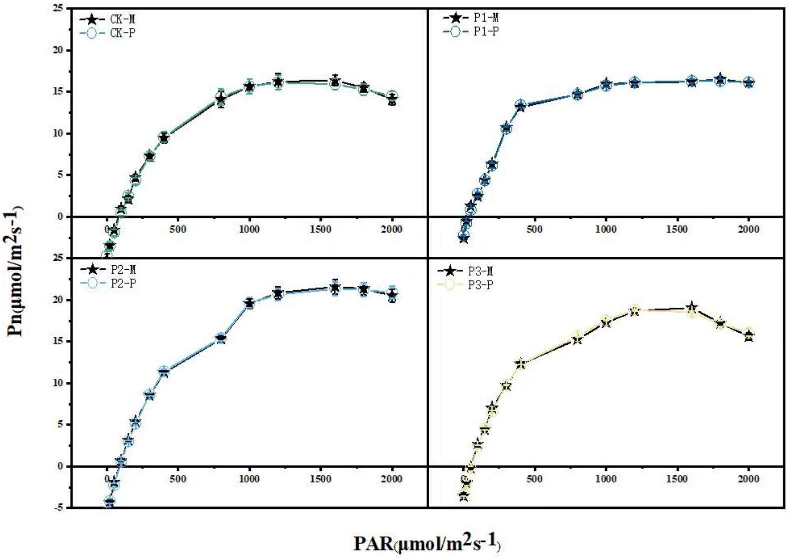

Fig. 5. Light response curve of *Convolvulus ammannii* for different moisture treatments

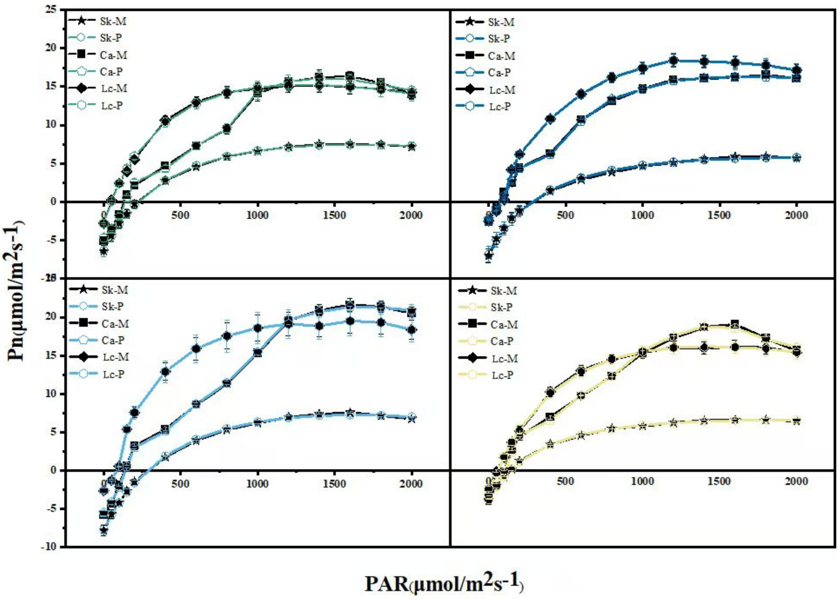

Fig. 6. Light response curves of three dominant plants with different moisture treatments

Note: *Stipa kryloyii* (Sk), *Leymus chinensis* (Ca), *Convolvulus ammannii* (Lc).
(M measured point, P predicted value)

As shown in Figures 3, 4, and 5, the photosynthetic response curves of the three dominant species under different treatments can all be well fitted by the rectangular hyperbolic model. The photosynthetic parameters of *Stipa kryloyii* under different treatments were calculated using the rectangular hyperbolic model. The results show that changes in precipitation affect the photosynthetic parameters of *Stipa kryloyii*, but only the maximum net photosynthetic rate (Pnmax) shows significant differences. Specifically, the average maximum net photosynthetic rate (Pnmax) of *Stipa kryloyii* in the control group (CK) is 7.059 μmol m^{-2} s^{-1}, while in treatments P1, P2, and P3, the values are 5.893 μmol m^{-2} s^{-1}, 7.404 μmol m^{-2} s^{-1}, and 6.615 μmol m^{-2} s^{-1}, respectively, showing P2 > CK > P3 > P1, with P2 and CK being significantly higher than P1.

As shown in Figure 4, the photosynthetic parameters of *Leymus chinensis* under different treatments were calculated using the rectangular hyperbolic model. The results show that precipitation changes affect the photosynthetic parameters of *Leymus chinensis*, but these changes are not statistically significant.

As shown in Figure 5, the photosynthetic response curves of *Convolvulus ammannii* under different treatments can also be well fitted using the rectangular hyperbolic model. The results show that P2 > P3 > P1 > CK, especially the Pmax under the P2 treatment, which is significantly higher than that in the CK and P1 treatments. The average light saturation point (LSP) under CK, P1, P2, and P3 treatments are 1392.479 μmol m^{-2} s^{-1}, 1764.182 μmol m^{-2} s^{-1}, 1607.32 μmol m^{-2} s^{-1}, and 1218.963 μmol m^{-2} s^{-1}, respectively, showing P1 > P2 > CK > P3, where P1 is significantly higher than CK and P3. The light compensation point (LCP) is 89.166 μmol m^{-2} s^{-1} for CK, 47.293 μmol m^{-2} s^{-1} for P1, 88.914 μmol m^{-2} s^{-1} for P2, and 53.754 μmol m^{-2} s^{-1} for P3, with CK > P2 > P3 > P1, where P2 and CK are significantly higher than P1. The dark respiration rate (Rd) follows the trend of P2 > CK > P3 > P1, and the initial quantum efficiency (α) follows P2 > P3 > CK > P1, with P2 being significantly higher than P1.

As shown in Figure 6, a comparison of the photosynthetic parameters of the three dominant plants reveals that under different precipitation treatments, the maximum net photosynthetic rate (Pn) of Stipa kryloyii is significantly lower than the other two species ($P < 0.05$). The light saturation point (LSP) under different treatments is higher than in the other two species, reaching significant levels under the P3 treatment ($P < 0.05$). The initial quantum efficiency (α) is lower than that of the other two species.

3.2 Plant Leaf Gas Exchange Parameters Response to Controlled Watering in the Non-Growing Season

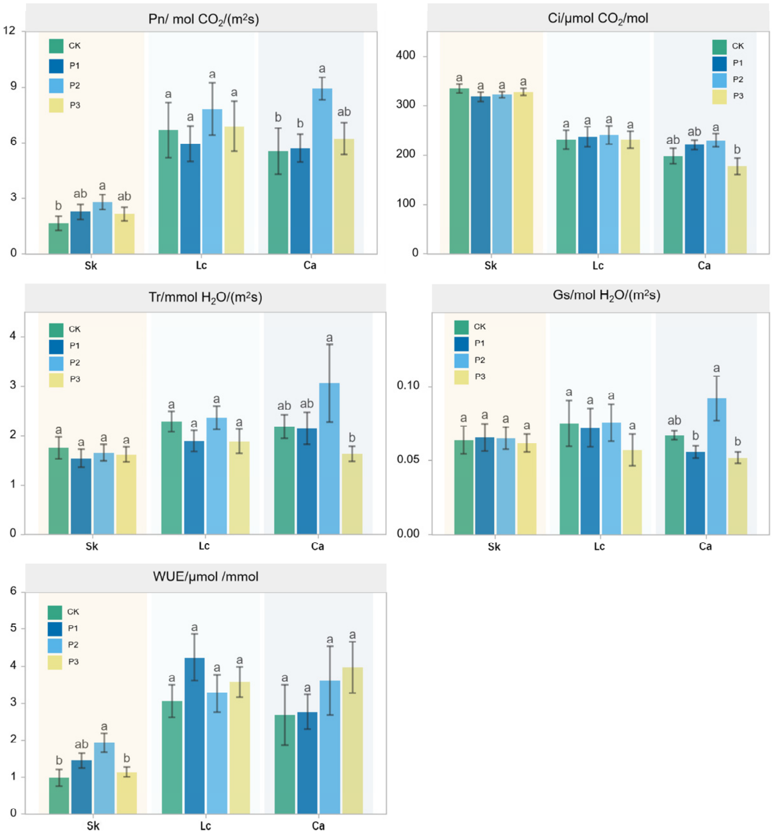

Fig. 7. Differences in Instantaneous Photosynthetic Parameters of Three Dominant Plants Under Different Watering Treatments

Under different precipitation treatments, significant differences were observed in the photosynthetic rate, intercellular CO_2 concentration, transpiration rate, stomatal conductance, and water use efficiency of the leaf tissues of the three dominant plant species (Figure 7). Among them, the photosynthetic rate of Stipa kryloyii and *Convolvulus ammannii* showed significant differences ($P<0.05$). Under the P2 treatment, the photosynthetic rate of Stipa kryloyii was significantly higher than that of CK ($P<0.05$). Under the P2 treatment, the photosynthetic rate of *Convolvulus ammannii* was significantly higher than that of CK and P1 ($P<0.05$). *Leymus chinensis* and *Convolvulus ammannii* exhibited higher photosynthetic abilities compared to *Stipa kryloyii*. The intercellular CO_2 concentration of *Convolvulus ammannii* showed significant differences ($P<0.05$), with P1 and P2 treatments resulting in significantly higher intercellular CO_2 concentrations than CK ($P<0.05$). The intercellular CO_2 concentrations of *Stipa kryloyii* and *Leymus chinensis* were relatively stable. The transpiration rate of *Convolvulus ammannii* also showed significant differences ($P<0.05$), with the highest transpiration rate under P1 treatment, significantly higher than P3 ($P<0.05$). The stomatal conductance of *Convolvulus ammannii* also exhibited significant differences ($P<0.05$), with the highest stomatal conductance under P1 treatment, significantly higher than P2 and P3 ($P<0.05$). The water use efficiency of *Stipa kryloyii* showed significant differences ($P<0.05$).

4 Discussion

4.1 Comparison of Light Response Curves of Three Dominant Plants Under Different Precipitation Treatments in the Non-Growing Season

In this study, the light response curves of the three dominant plants were well fitted by a hyperbolic model (Figure 4). Under low light conditions (light intensity ≤ 400 μmol m^{-2} s^{-1}), the photosynthetic rate (Pn) of all treatments showed a rapid increase with the increase in photosynthetically active radiation (PAR), followed by a plateau, exhibiting characteristics of a saturation-type light response curve under high light. At high PAR, the photosynthetic rate of the plants was suppressed, and the degree of suppression varied among the species [14]. The maximum net photosynthetic rate (Pnmax) reflects the plant's maximum photosynthetic ability, while the initial quantum efficiency (α) reflects the plant's ability to absorb, convert, and utilize weak light during photosynthesis. The light saturation point (LSP) and light compensation point (LCP) represent the plant's ability to utilize strong and weak light, respectively. A higher LSP and a lower LCP indicate stronger light adaptation capabilities, while the opposite suggests weaker light adaptation ability [15].

Upon analyzing the light response curves of the three plants under different precipitation treatments, it was found that these plants exhibited varying sensitivities to non-growing season precipitation. Compared to the control group, *Convolvulus ammannii* under P2 treatment showed stronger photosynthetic potential. Under P1 treatment, Conolvulus *ammannii* had the highest light saturation point, the lowest initial quantum efficiency (α), light compensation point (LCP), and dark respiration rate (Rd), indicating that, relative to other treatments, it had stronger adaptation to high light but weaker adaptation to low light. Among the three species, *Stipa kryloyii* had a much lower maximum net photosynthetic rate (Pn) than the other two dominant species ($P<0.05$), but its light saturation point (LSP) was consistently higher than the other two species under all treatments ($P<0.05$), indicating that *Stipa kryloyii* is better adapted to high light environments. The initial quantum efficiency (α) and light compensation point (LCP) reflect the plant's ability to utilize weak light. Research has shown that under suitable conditions, the α value of most plants ranges between 0.03-0.05. In this study, the α values for *Stipa kryloyii, Leymus chinensis*, and *Convolvulus ammannii* ranged from 0.039-0.045, 0.053-0.073, and 0.053-0.07, respectively. The LCP values ranged from 133.111-273.341 μmol m^{-2} s^{-1}, 40.276-63.675 μmol m^{-2} s^{-1}, and 47.293-89.167 μmol m^{-2} s^{-1}, respectively. This indicates that, under low light, *Leymus chinensis* and *Convolvulus ammannii* have higher light utilization efficiency, and their dark respiration rates (Rd) are lower than that of *Stipa kryloyii*, suggesting that these plants use fewer photosynthetic products for respiration.

4.2 Effects of Non-Growing Season Precipitation Changes on Plant Leaf Photosynthesis

Studies have shown that increased precipitation can enhance plant leaf photosynthetic efficiency [16, 17], and changes in water supply have a significant impact on plant stomatal conductance. Stomata serve as the main gas exchange channels for plant leaves at the microscopic scale, affecting both photosynthesis and transpiration processes and controlling the dynamic balance of carbon and water within the plant. Stomatal activity is a critical mechanism for plants to adapt to fluctuating environmental conditions. When stomata open wider, CO_2 enters the leaf cells, promoting carbon fixation. At the same time, however, this increases water loss. When plants are under water stress, stomata will close to reduce water loss. Song et al. [18] found that increased precipitation improved photosynthesis in grassland plants such as *Stipa breviflora* and *Convolvulus ammannii*, but also slightly reduced their water use efficiency (WUE). Zhou et al. [19] studied *Artemisia scoparia* and found that under drought stress, the leaf transpiration rate and stomatal conductance significantly decreased, while water use efficiency increased. Yu et al. [20] found that under insufficient precipitation, trees close their stomata to reduce water evaporation, thereby improving water use efficiency. In this study, based on a controlled watering experiment in a desert steppe during the non-growing season, we found that increased water supply during the non-growing season had varying effects on the photosynthesis of *Stipa kryloyii* and *Convolvulus ammannii*. Under the P2 treatment, *Stipa kryloyii* showed a significant increase in net photosynthetic rate and long-term instantaneous water use efficiency ($P<0.05$). The improvement in WUE reflects the plant's ability to produce more carbon assimilation products per unit of water consumed [21], suggesting that increased water during the non-growing season promoted the accumulation of organic matter in *Stipa kryloyii*. *Convolvulus ammannii* is a deep-rooted plant with roots that can grow down to the calcareous layer, even reaching a depth of 75 cm [22]. In this study, under the P2 treatment, the net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration of *Convolvulus ammannii* all increased to varying degrees, indicating that substantial water increase during the non-growing season also influenced the water-carbon activity of deep-rooted plants.

The results also show that the response of *Leymus chinensis*' photosynthetic physiological characteristics to changes in precipitation during the non-growing season was not significant. This suggests that *Leymus chinensis* may have a weaker sensitivity to precipitation changes during the non-growing season compared to the other two dominant species, and its water use strategy might differ from that of the other species[23].

5 Conclusion

By conducting controlled water experiments during the non-growing season, we found that changes in precipitation during this period could have varying effects on the three dominant species of desert steppes. These effects included changes in the plant's light energy utilization efficiency and photosynthetic intensity, which had not been fully revealed in previous studies. Moreover, we found that the response of the photosynthetic functions of different dominant species to changes in non-growing season precipitation varied. Some plants showed significant changes in their photosynthetic physiological parameters due to changes in non-growing season precipitation, while in other plants, no significant changes were observed. This reflects differences in the sensitivity of different dominant species to climate change and suggests that they may have adopted different adaptive strategies. Given the increasing impact of climate change, research on the adaptive mechanisms of fragile ecosystems, such as desert steppes in Inner Mongolia, is of great significance. Our study provides valuable experimental evidence for assessing the impacts of climate change in ecologically fragile grassland areas. Future research will focus on using multi-factorial and process-based studies to further elucidate the mechanisms behind the effects of non-growing season precipitation on plant water-carbon utilization activities.

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