Research article

Nitrogen application mitigates drought-induced metabolic changes in *Alhagi sparsifolia* seedlings by regulating nutrient and biomass allocation patterns

Zhihao Zhang [a,b,c,d], Akash Tariq [a,b,c,*], Fanjiang Zeng [a,b,c,**], Corina Graciano [e], Bo Zhang [a,b,c]

[a] *Xinjiang Key Laboratory of Desert Plant Roots Ecology and Vegetation Restoration, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, 830011, China*
[b] *State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, 830011, China*
[c] *Cele National Station of Observation and Research for Desert-Grassland Ecosystems, Cele, 848300, China*
[d] *University of Chinese Academy of Sciences, Beijing, 10049, China*
[e] *Instituto de Fisiología Vegetal, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de La Plata, Buenos Aires, Argentina*

ABSTRACT

Groundwater and its associated nutrients sustain the establishment and persistence of phreatophytes. Rapid root elongation immediately after germination is vital for desert species to access deep water sources to avoid water-deficit stress. However, the growth strategy and responses to nutrients and water of young phreatophyte seedlings before their roots reach the water table are poorly understood, especially in the scenarios of nitrogen (N) deposition and drought. We investigated how simulated N deposition and drought affect the plasticity of *Alhagi sparsifolia* seedlings by multiple eco-physiological mechanisms. Seedlings were planted under drought-stressed or well-watered conditions and subjected to various levels of N addition (0, 3.0, 6.0, or 9.0 gN·m^{-2} yr^{-1}). The amounts of N and water independently or interactively affected the photosynthetic traits, drought tolerance characteristics, morphological traits, biomass allocation strategy, and nutrient distribution patterns among the plant organs. Moreover, changes mediated by N addition at the leaf level reflected the drought acclimation of the seedlings, which may be related to biomass and nutrient partitioning between organs. The roots were found to be more sensitive to variation of the N:phosphorus (P) ratio, and greater proportions of biomass, N, and P were allocated to resource-acquiring organs (i.e., leaves and fine roots) than to other tissues. *A. sparsifolia* adopts numerous strategies to tolerate drought, and additional N input was crucial to enhance the growth of drought-stressed *A. sparsifolia*, which was mainly attributable to its positive impact on the N and P uptake capacity mediated by increased biomass allocation to the roots.

1. Introduction

Nutrients and water are essential factors for sustaining plant growth. These two components of the water table are crucial for the establishment and persistence of phreatophytes in desert ecosystems (Arndt et al., 2004). Rapid root elongation is imperative for phreatophytes to obtain groundwater resources and minimize the risk of water and nutrient deficiency to adapt to arid environments (Canham et al., 2015). However, resource requirements vary with plant development, such as in the case of newly germinated seedlings, which are particularly susceptible to water stress (Evans and Etherington, 1991; McDowell et al., 2008). In hyperarid ecosystems, shallow soil moisture and the availability of nutrients such as nitrogen (N) are extremely limited, which severely inhibits the natural germination of phreatophyte seeds. Spontaneous seedling emergence is rare for phreatophytes (Liu et al., 2013a), which threatens natural vegetation renewal. Therefore, it is important to understand the growth strategies of young phreatophyte seedlings in response to nutrient and water availability before their roots reach the water table.

Abbreviations		NiR	nitrite reductase (EC 1.7.7.1)
		NR	nitrate reductase (EC 1.6.6.1)
AN	available N	P	phosphorus
AIC	Akaike Information Criterion	PBS	phosphate buffer saline;
AP	available P; BM, biomass	P_n	net photosynthesis rate
Chl	Chlorophyll; diam, diameter	R/S	root/shoot ratios
E	transpiration rate	SBD	stem base diameter
EC	electrical conductivity	SLA	specific leaf area
EDTA	ethylene diamine tetraacetic acid	SOC	soil organic carbon
F_v/F_m	the maximum quantum efficiency of photosystem II	SOD	superoxide dismutase
g_s	stomatal conductance	SP	soluble proteins
LRWC	Leaf relative water content	SS	soluble sugars
LSD	the least significant difference	SWC	soil water content
LT	leaf thickness	TBA	thiobarbituric acid
MDA	malondialdehyde	TCA	trichloroacetic acid
N	nitrogen	WUE	water use efficiency; yr, year
NBT	nitroblue tetrazolium		

Desert species can coordinate their various organs with respect to the absorption and distribution of limited resources (e.g., N and phosphorus (P)) to adapt to dry conditions (Liu et al., 2010). In plant tissues, N and P are key components of proteins and nucleic acids, respectively, which are involved in numerous essential roles in photosynthesis, respiration, the transformation and storage of photosynthates, chemical defense, and other functions (Vrede et al., 2004). Variation of the N:P ratio can occur as one aspect of physiological plasticity in response to a changing environment. For example, desert species may allocate higher N concentrations to their leaves to better adapt to the arid climate by exploiting the abundant light (Palmroth et al., 2013), altering leaf traits (Wright et al., 2001), and enhancing water-use efficiency (Wright et al., 2003). Furthermore, plants respond to environmental fluctuations by altering the allocation of biomass among their different organs to meet the requirements for water and nutrient capture and maximize their growth (Bloom et al., 1985; Chapin et al., 1987). According to optimal partitioning theory, in nutrient-limited environments plants allocate more biomass belowground, whereas in nutrient-rich environments they shift more biomass aboveground (Poorter et al., 2012). Elucidating the biomass allocation patterns of desert plants is essential for understanding their adaptive strategies. For example, under increased drought stress, desert shrubs preferentially allocate biomass to the roots to capture groundwater, whereas ephemeral species allocate a large proportion of biomass to the growth of aboveground parts to rapidly complete their life cycle (Cheng et al., 2019).

The N deposition rate, which is affected by anthropogenic activities, in northwestern China is predicted to reach 2.5 $gN{\cdot}m^{-2}$ yr^{-1} by 2030 (Liu et al., 2013b). Increased N deposition has changed soil nutrient status and altered the function and structure of some desert ecosystems (Ladwig et al., 2012; Zhao et al., 2019). The improved soil N availability mediated by moderate N input can stimulate plant growth (Zhao et al., 2019), and increased foliage N content in response to higher N deposition can be beneficial for improving photosynthetic capacity (Wright et al., 2001). However, the adverse impacts induced by high N load could increase the vulnerability of plants to other types of stress (Zhang et al., 2017), such as drought. The foliage N:P ratio has been widely applied as an indicator of soil nutrient limitation for herbaceous and woody species (Koerselman and Meuleman, 1996), which is appropriate for ecosystems with superior water and nutrient conditions. Nevertheless, roots may be more sensitive to environmental fluctuations than leaves in desert ecosystems where nutrients and water are scarce. To date, the response of desert species to simulated N deposition and water stress has been widely reported. However, most previous studies have preferentially focused on morphological and physiological characteristics (Fan et al., 2013; Ladwig et al., 2012) and the patterns of nutrient partitioning and biomass allocation (Fisher et al., 1988; Li et al., 2016). Given that the adaptability of plants is a complex process, data obtained using a limited set of indicators may be influenced by plant genotype variation, leading to unreliable results. Therefore, it is crucial to understand plant adaptation strategies by evaluating multiple comprehensive indices and exploring the generality of patterns and trade-offs across numerous plant species. From a life-cycle perspective, studying the morphological and physiological performance and the active allocation of nutrients and biomass among the organs of young phreatophyte seedlings is anticipated to improve our understanding of adaptation strategies in hyperarid ecosystems under increasingly elevated N deposition.

Alhagi sparsifolia Shap. is a dominant spiny phreatophyte shrub belonging to the Fabaceae family that is distributed in the desert–oasis transition zone of northwestern China and Central Asia and plays a crucial role in sand stabilization and animal husbandry (Arndt et al., 2004; Zeng et al., 2013). In recent years, *A. sparsifolia* has been exposed to increasing N deposition and drought stress. Thus, in this study, we aimed to address the following research objectives: (1) to explore the eco-physiological mechanisms underlying the responses of young (one-year-old) *A. sparsifolia* seedlings to different levels of N addition and water regimes, and (2) to determine whether simulated N deposition negatively influences the performance of *A. sparsifolia* seedlings. We thus investigated the manner in which the exchange parameters, photochemistry, drought tolerance characteristics, morphological traits, biomass allocation, and nutrient distribution patterns among different organs in *A. sparsifolia* seedlings respond to simulated N deposition and water stress. We hypothesized the following: (1) the adverse effects of drought stress on the physiological performance of seedlings may be alleviated by moderate N input, (2) N addition and drought alter the allocation patterns of biomass and nutrients, and (3) the N:P ratio of the roots may be a potential bioindicator of N deposition. Testing these hypotheses is anticipated to contribute to elucidating the adaptation strategies of *A. sparsifolia* seedlings under increased N deposition and drought conditions and reveal the risks associated with elevated N deposition on desert ecosystems dominated by *A. sparsifolia*.

2. Materials and methods

2.1. Experiment design

The study site was located at the Cele National Station of Observation and Research for Desert-Grassland Ecosystem (37°00′56″ N, 80°43′81″ E), Chinese Academy of Sciences, at the southern edge of the Taklamakan Desert, the second-largest mobile desert in the world, and on the

northern slope of the Qinghai–Tibet Plateau, which is also known as the world's third pole. In this area, the mean annual precipitation, maximum evaporative potential, and average yearly temperature are approximately 35 mm, 2600 mm, and 11.9 °C, respectively. The sparse vegetation consists of phreatophyte species dominated by *A. sparsifolia* (Zeng et al., 2016).

The pot experiment was conducted in an outdoor nursery from May to August 2019. All seeds were collected randomly from the natural desert–grassland transition zone (36°17′–39°30′ N, 80°03′–82°10′ E). At least ten seeds were sown in each pot (90 L volume, 40 cm bottom diameter, 50 cm top diameter, and 62 cm height) in May 2019 after watering the soil to the maximum field capacity (ca. 18%). Fifty kilograms of homogenized topsoil from the study area (0–30 cm depth; aeolian loamy sand with the following physicochemical properties: total N, 0.23 g kg^{-1}; organic C, 2.99 g kg^{-1}; total K, 23.11 g kg^{-1}; total P, 0.60 g kg^{-1}) were used in this study. After four weeks of growth with regular management, the seedlings were thinned out to give one healthy and uniform seedling (3.5 ± 0.5 cm height, 4–6 leaves) in each pot.

As the focus of this study was seedling growth rather than survival, we considered that watering once per day was necessary to ensure that the seedlings remained alive throughout the course of the experiment. We controlled the amount of water delivered to individual pots. For the first four weeks, all of the pots received approximately 1.5 L of water. For the subsequent period, well-watered pots still received approximately 1.5 L of water per day, whereas simulated drought pots received approximately 0.5 L of water per day. Individual pots were placed on plastic trays to eliminate the transfer of material between pots. After water addition at 7:00 p.m. each day, the pots were rearranged randomly to minimize the influence of potential environmental heterogeneity. A canopy made of transparent plastic film was used to cover the pots when it rained. A conspicuously high N deposition rate (2.5 gN·m^{-2} yr^{-1}) will exist in northwestern China by 2030 owing to rapid agricultural and industrial development (Liu et al., 2013b). Furthermore, atmospheric N deposition is expected to double by 2050 (Galloway et al., 2008). We also previously simulated the extreme levels of N deposition in the North China Plain, where the rate is 9.0 gN·m^{-2} yr^{-1} (Liu et al., 2013b). Therefore, we investigated four N treatments (N0, 0 gN·m^{-2} yr^{-1}; N1, 3.0 gN·m^{-2} yr^{-1}; N2, 6.0 gN·m^{-2} yr^{-1}; and N3, 9.0 gN·m^{-2} yr^{-1}) with six replicates of each treatment under both water regimes. The simulated N deposition (solid urea) was applied once per month between June and August 2019 to the upper surface after watering.

2.2. Sample collection

Plant samples were collected in late August 2019 during the mid-to-late growth period. Three to five *A. sparsifolia* seedlings with a similar growth status were selected, and the fully expanded leaves of each plant were used for gas exchange and chlorophyll fluorescence measurements. The leaves were then picked, placed in resealable bags, and immediately stored at −80 °C for subsequent laboratory analysis.

2.3. Gas exchange and chlorophyll fluorescence measurements

The net photosynthesis rate (P_n), stomatal conductance (g_s), and transpiration rate (E) were measured using a portable photosynthesis system (LI-6400, LI-COR Inc., USA) between 9:00 and 11:00 a.m. The relative humidity of the air, CO_2 concentration, and photon flux density were maintained at 30–40%, 400 μmol mol^{-1}, and 1300 μmol m^{-2} s^{-1} in all cases. The water-use efficiency (WUE) was calculated using the following equation: P_n/E. Using the same leaves, the maximum quantum efficiency of photosystem II (F_v/F_m) was then measured with a Handy Plant Efficiency Analyzer (Hansatech, UK) after 30 min of dark acclimation at ambient air temperature and application of a saturation light pulse of 1500 μmol m^{-2} s^{-1} for 0.8 s.

2.4. Photosynthetic pigment measurements

Chlorophyll was extracted from samples of fresh leaves (0.1–0.3 g) using 95% (v/v) ethanol. Then, the absorbance of the filtered extract was measured at 665 nm and 649 nm, and the chlorophyll content (mg·g^{-1}) was calculated according to the following equations of Lichtenthaler and Wellburn (1983). The final units were converted to mg·g^{-1} dry weight (DW).

$$\text{Chl a} = 13.98A_{665} - 6.88A_{649} \tag{1}$$

$$\text{Chl b} = 24.96A_{649} - 7.32A_{665} \tag{2}$$

$$\text{Chl a+b} = \text{Chl a} + \text{Chl b} \tag{3}$$

$$\text{Chl a/b} = \text{Chl a / Chl b} \tag{4}$$

2.5. Measurement of biochemical parameters

The soluble protein (SP) concentration in extracts obtained from fresh leaves (0.1–0.3 g) was determined using Coomassie Brilliant Blue G-250 with bovine serum albumin as the standard (Bradford, 1976). The soluble sugar (SS) concentration was determined via the anthrone method (Yemm and Willis, 1954) with glucose as the standard. The free proline content was measured using ninhydrin according to the method of Bates et al. (1973). Lipid peroxidation was measured as the malondialdehyde (MDA) concentration via the thiobarbituric acid (TBA) method with some modifications (Heath and Packer, 1965). Samples of frozen leaves (0.1 g) were ground in a mortar and pestle with liquid nitrogen and 5 mL of 10% trichloroacetic acid (TCA) to obtain a homogeneous powder. The homogenate was centrifuged at 8000 ×g and 4 °C for 10 min, then 0.1 mL of the supernatant was mixed with 0.3 mL of 0.6% TBA in 10% TCA and the resulting solution was heated at 95 °C for 30 min, cooled to room temperature in an ice bath, and centrifuged at 10,000 ×g for 10 min. Finally, the absorbance was measured at 450, 532, and 600 nm. The MDA content was calculated according to the following equation and then expressed as nmol·g^{-1} fresh weight (FW):

$$\text{MDA (nmol·L}^{-1}) = 6.45 \, (A_{532} - A_{600}) - 0.56A_{450} \tag{5}$$

The ground leaves were homogenized under ice-cold conditions in 1.0 mL of 0.1 M phosphate buffer (pH 7.4) containing 0.5 mM ethylenediaminetetraacetic acid (EDTA). The homogenate was then centrifuged at 8000 ×g and 4 °C for 10 min. The superoxide dismutase (SOD) activity was determined by measuring the rate of reduction of nitroblue tetrazolium (NBT) at 560 nm (Giannopolitis and Ries, 1977). One unit of SOD activity was defined as the enzyme concentration that inhibited the reduction of NBT by 50%.

To evaluate the nitrate reductase (NR, EC 1.6.6.1) activity, 0.1 g samples of frozen leaves were first homogenized in 1.0 mL of 25 mM phosphate-buffered saline (PBS, pH 8.7) containing 10 mM cysteine and 1 mM EDTA, and the homogenate was then centrifuged at 4000 ×g and 4 °C for 10 min. The NR activity of the supernatant was then determined over ice via the diazo coupling method with the Griess reagent (Sánchez-Rodríguez et al., 2011). The nitrite reductase (NiR, EC 1.7.7.1) activity was determined by measuring the disappearance of NO_3^- in the presence of the Griess reagent at 520 nm (Lillo, 1984). Frozen samples (0.1 g) were homogenized in 2 mL of 50 mM Tris-HCl buffer (pH 7.8) containing 15% glycerol, 0.1% Triton X-100, 1 mM EDTA, and 14 mM 2-mercaptoethanol and then centrifuged at 10,000 ×g and 4 °C for 10 min.

2.6. Leaf relative water content (LRWC), biomass, and growth measurements

The FW of fully expanded leaves collected from each pot was

measured using an electronic balance, and then the leaf samples were soaked in distilled water in the dark at 4 °C for 4 h. The samples were then weighed to determine their turgid weight (TW) and subsequently transferred to an oven at 70 °C for 24 h prior to measuring their DW. The LRWC values of the samples were determined using the following equation:

$$LRWC = [(FW - DW)/(TW - DW)] \times 100\% \qquad (6)$$

A Vernier caliper was used to measure the stem base diameter (SBD) and leaf thickness (LT). The leaf area was measured using the ImageJ 1.52t software (Softonic International, Spain) according to the standard procedure. The specific leaf area (SLA) was calculated by dividing the leaf area by the leaf DW. Fine and coarse roots were manually sorted after removing the soil via washing. Then, each plant was split into various sections, namely, leaf, thorn (assimilating shoot), stem, coarse root (>2 mm diameter), and fine root (<2 mm diameter), which were dried at 70 °C for 24 h prior to measuring the DW. Furthermore, the biomass allocation among organs was calculated by dividing the biomass of a specific organ by the total plant biomass. The root/shoot (R/S) ratio was calculated from the biomass of the aboveground and belowground parts.

2.7. Plant chemical analysis and nutrient allocation

The organ samples (leaves, stems, coarse roots, and fine roots) were milled to fine powders (<0.15 mm) using a ball mill for measurement of the N and P concentrations. Following digestion with concentrated H_2SO_4, the N and P concentrations in the digests were determined using a Kjeldahl Nitrogen Analyzer (K1160, Jinan Hanon Instruments Co. Ltd., China) and an inductively coupled plasma optical emission spectrometer (iCAP 6300, Thermo Elemental, USA), respectively. The N or P content of a particular organ was calculated according to Eq. (7). The distribution ratios of the two nutrients in each organ were calculated by dividing the nutrient mass in that organ by the total nutrient mass in the plant.

N (or P) mass of the specific organ = N (or P) concentration × specific organ biomass   (7)

2.8. Measurement of soil physicochemical properties

Soil samples were collected in triplicate from three layers of the pots (upper, 0–20 cm; middle, 20–40 cm; bottom, 40–60 cm), and each sample was then divided into three subsamples. The first subsample was dried at 105 °C to determine the soil water content (SWC). The second subsample was air dried and then sifted through a 0.15 mm sieve prior to determination of its chemical properties. The content of soil organic carbon (SOC) was evaluated via the $K_2Cr_2O_7/H_2SO_4$ oxidation method. The total N (TN) concentration was determined using a Kjeldahl Nitrogen Analyzer (K1160, Jinan Hanon Instruments Co. Ltd., China). The available N (AN) concentration was measured via the alkaline hydrolysis method. The total P (TP) and total K (TK) contents were determined via inductively coupled plasma optical emission spectrometry (iCAP 6300, Thermo Elemental, USA) after sample digestion in concentrated HNO_3. The available P (AP) was extracted using HCl/NH_4F and determined colorimetrically via the ascorbic acid/molybdate method using a continuous-flow autoanalyzer. The available K was extracted using NH_4OAc and measured. The soil pH was measured at a soil:water ratio of 1:2.5 (w/v) using a pH meter (PHSJ-6L, INESA Scientific Instrument Co. Ltd., China). The electrical conductivity (EC) was measured at a soil:water ratio of 1:5 (w/v) using an EC meter (DDSJ-319L, INESA Scientific Instrument Co. Ltd., China). The third subsample was used for spectrophotometric determination of the mineral soil N (NO_3^-–N and NH_4^+–N) content according to the method described by Bremner and Mulvaney (1982). The final results are presented in Table S1.

2.9. Statistical analyses

Statistical analyses were performed using the R software (Team, 2013). The normality of the raw data was assessed using the Shapiro–Wilk normality test. Analysis of variance (ANOVA) was performed to determine the significance of the effects of N and water addition and their combination on plant eco-physiological parameters and soil properties. If a factor or combination was significant ($P < 0.05$), the means were compared using the least significant difference (LSD). Multiple regressions were performed using the InfoStat 2018 software (Di Rienzo et al., 2018) by running all of the possible models, and the estimated parameters from the model with the lowest Akaike information criterion (AIC) are reported. Figures were generated using the ggplot2 package in R.

3. Results

3.1. Photosynthetic parameters

We found that both N and the combination of water and N exerted a significant influence on the P_n, g_s, and E values of *A. sparsifolia* seedlings (Fig. 1), while the WUE was affected only by N. Compared with the N0 group, N application significantly increased the P_n, irrespective of the water regime, and the highest value of P_n among all of the treatments was observed for the N1 group (3 gN·m^{-2} yr^{-1}) under simulated drought conditions. The N2 group (6 gN·m^{-2} yr^{-1}) displayed significantly increased g_s and E values under simulated drought conditions. Similarly, the N2 and N3 (9 gN·m^{-2} yr^{-1}) groups exhibited higher g_s and E values than the N0 group under well-watered conditions. However, only the N1 group displayed a significantly increased WUE.

3.2. Chlorophyll fluorescence measurements

No significant effect of N, water, or their combination on the indicators of the levels of photosynthetic pigments, namely, chlorophyll (Chl) a, Chl b, Chl a+b, and Chl a/b, was observed. However, we did observe a significant influence of both N and water, but not their combination, on the maximum quantum efficiency of photosystem II (F_v/F_m) for the *A. sparsifolia* seedlings (Fig. 3). F_v/F_m was highest for the N3 group, and it was reduced by drought stress.

3.3. Levels of antioxidant enzymes, N-assimilation-related enzymes, osmolytes, and soluble protein

We observed significant effects of N and the combination of N and water on the levels of SP, SOD, and NiR (Fig. 4). N application markedly increased the SP content other than N3 treatment under drought conditions. Elevated SOD activities were also observed upon N addition under both water regimes, although a reduction in the activity of SOD was observed in N3 treated well-watered group. Furthermore, N addition improved the NiR activities of the drought-stressed seedlings, whereas it did not exert any significant influence on the NiR activities under well-watered conditions. The amount of N addition, water regime, and their combination were found to considerably influence the SS, proline, and NR levels. First, drought stress markedly improved SS accumulation in the leaves. A decreasing trend in the SS content of the drought-stressed seedlings with increasing N addition was observed, while the N2 and N3 groups also displayed reduced SS contents under the well-watered regime. An increased proline content was observed in the drought-stressed seedlings. Similar to the variation in the SS content, a reduction in the proline content with increasing N addition was observed under simulated drought conditions, while the N2 and N3 groups also exhibited decreased proline contents under the well-watered regime. Furthermore, we observed lower NR activities in the drought-stressed seedlings. N addition significantly decreased the NR activity under simulated drought conditions, whereas the NR activity first
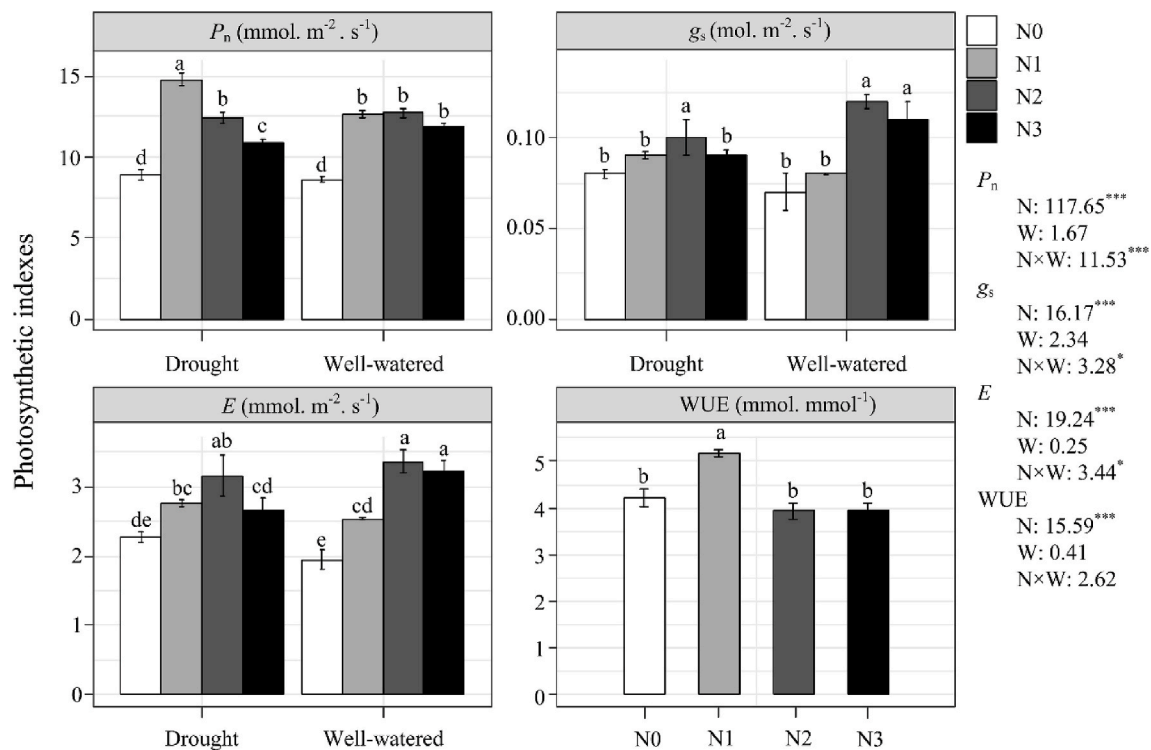
Fig. 1. Effects of nitrogen deposition (N) and water (W) treatments on gas exchange parameters in *Alhagi sparsifolia* seedlings leaves. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 $gN.m^{-2}.yr^{-1}$ (N1), 6 $gN.m^{-2}.yr^{-1}$, 9 $gN.m^{-2}.yr^{-1}$ (N3). Bars show means ± SE (n = 5). Different letters above indicate significant differences ($P < 0.05$) among all treatments according to the least significant difference (LSD) test. A summary of the results of a two-way ANOVA addressing the effects of nitrogen and water treatments is seen in the right-hand corner of each panel. *, **, ***, indicate that F value were significant at $P \leq 0.05$, 0.01, 0.001, respectively.

increased and subsequently decreased with increasing N addition for the well-watered seedlings. Only N addition significantly affected the MDA content; compared to the N0 group, additional N markedly increased the MDA content.

3.4. Biomass and growth

We found that N, water, and their combination exerted significant effects on the amounts of biomass at both the organ and whole-plant levels (Fig. 5 and S1). Under both water regimes, the biomass of various organs and the entire plant first increased and then decreased with increasing N addition. Under simulated drought conditions and for the N1 and N2 groups under well-watered conditions, N addition profoundly improved the amounts of biomass in the leaves, thorns, coarse roots, fine roots, and entire plant. However, the N3 group did not display significant changes in the amounts of biomass in the leaves, stems, fine roots, and entire plant under well-watered conditions, while the amount of biomass in the thorns even decreased. The amounts of biomass in the leaves, stems, and coarse roots were highest for the N1 group under well-watered conditions, while the total biomass and amount of biomass in the fine roots were highest for the N2 group under simulated drought conditions. The R:S ratios exhibited an increasing trend with increasing N addition in the drought-stressed plants, whereas no significant change was observed in the well-watered plants.

N addition and water treatments caused significant variations in biomass allocation among the plant organs (Fig. 5). For the drought-stressed plants, the N2 and N3 groups displayed increased biomass allocation to the fine roots, whereas neither treatment altered the biomass allocation to the fine roots in the well-watered plants. N addition also markedly increased the biomass allocation to the leaves in the drought-stressed plants. Under well-watered conditions, the amount of biomass in the fine roots was relatively high compared to the other

organs. The N1 group displayed significantly decreased biomass allocation to the fine roots. Furthermore, the N1 and N3 groups exhibited increased biomass allocation to the coarse roots and decreased biomass allocation to the thorns for the well-watered plants.

We observed that N, water, and their combination exerted a significant influence on the SLA and LRWC (Table 1). Under simulated drought conditions, N addition noticeably increased the SLA and LRWC. The LT was affected by N addition independently of the water regime, with the N treatment groups displaying higher values compared to the control. Moreover, N addition and water, but not their combination, affected the SBD; the N1 and N2 groups exhibited significantly increased values, whereas no noticeable difference was observed between the N3 group and the control. Simulated drought conditions significantly reduced the SBD with respect to the well-watered plants.

3.5. N:P stoichiometry

Simulated N deposition and the water regime influenced the N and P concentrations and the allocation strategy in *A. sparsifolia* seedlings (Table S2, Fig. 6). The addition of N alone markedly altered the N concentration in the coarse roots and the P concentration in the fine roots (Tables S2 and S3). The addition of N and the water regime independently affected the N concentrations of the stems and leaves, while their combination altered the N:P ratio in the fine roots. The addition of N, the water regime, and their combination significantly affected the N concentration in the fine roots, the P concentrations in the stems and coarse roots, and the N:P ratio in the coarse roots.

The addition of N increased the relative N content at the plant level under both water regimes, with the exception of the N3 group under the well-watered regime (Fig. 6). The mass of N allocated to the stems by the drought-stressed seedlings displayed a decreasing trend with increasing N addition, whereas the amounts of N allocated to other organs
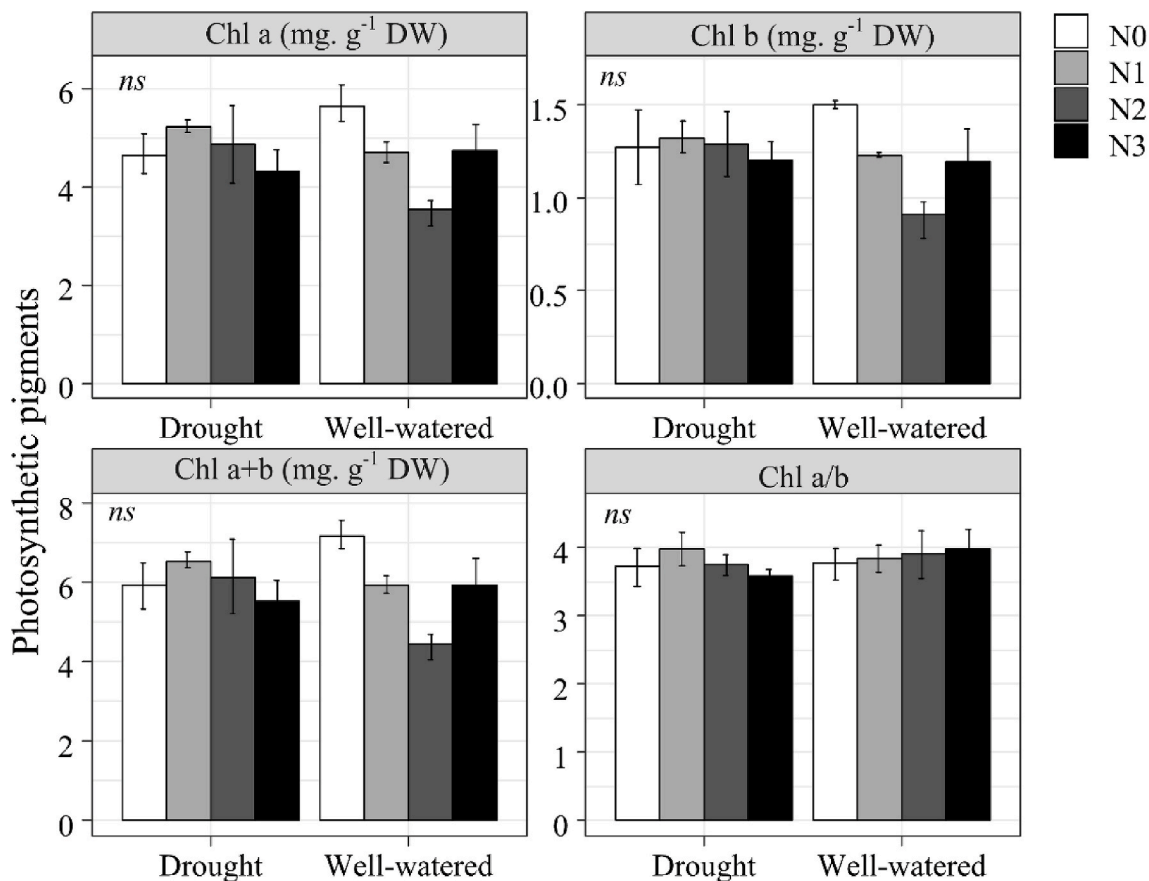
Fig. 2. Effects of nitrogen deposition (N) and water (W) treatments on chlorophyll parameters in *Alhagi sparsifolia* seedlings leaves. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 $gN.m^{-2}.yr^{-1}$ (N1), 6 $gN.m^{-2}.yr^{-1}$ (N2), 9 $gN.m^{-2}.yr^{-1}$ (N3). Bars show means $\pm$ SE (n = 3). There is no significant effect of water, nitrogen, or interaction. A summary of the results of a two-way ANOVA addressing the effects of nitrogen and water treatments is seen in the right-hand corner of each panel. *ns* denotes no significant difference.
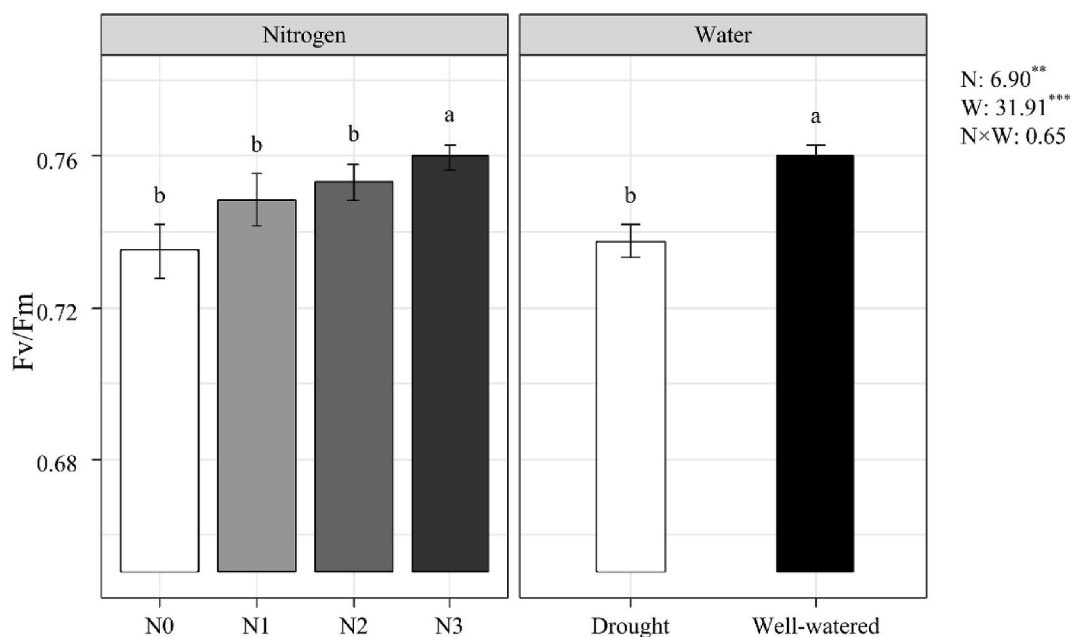

Fig. 3. Effects of nitrogen deposition (N) and water (W) treatments on the maximum quantum efficiency of photosystem II (F_v/F_m) of *Alhagi sparsifolia* seedlings leaves. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 $gN.m^{-2}.yr^{-1}$ (N1), 6 $gN.m^{-2}.yr^{-1}$ (N2), 9 $gN.m^{-2}.yr^{-1}$ (N3). Bars show means $\pm$ SE (n = 4). Different letters above indicate significant differences ($P < 0.05$) according to the least significant difference (LSD) test. A summary of the results of a two-way ANOVA addressing the effects of nitrogen and water treatments is seen in the right-hand corner. *, **, ***, indicate that *F* value were significant at $P \leq$ 0.05, 0.01, 0.001, respectively.
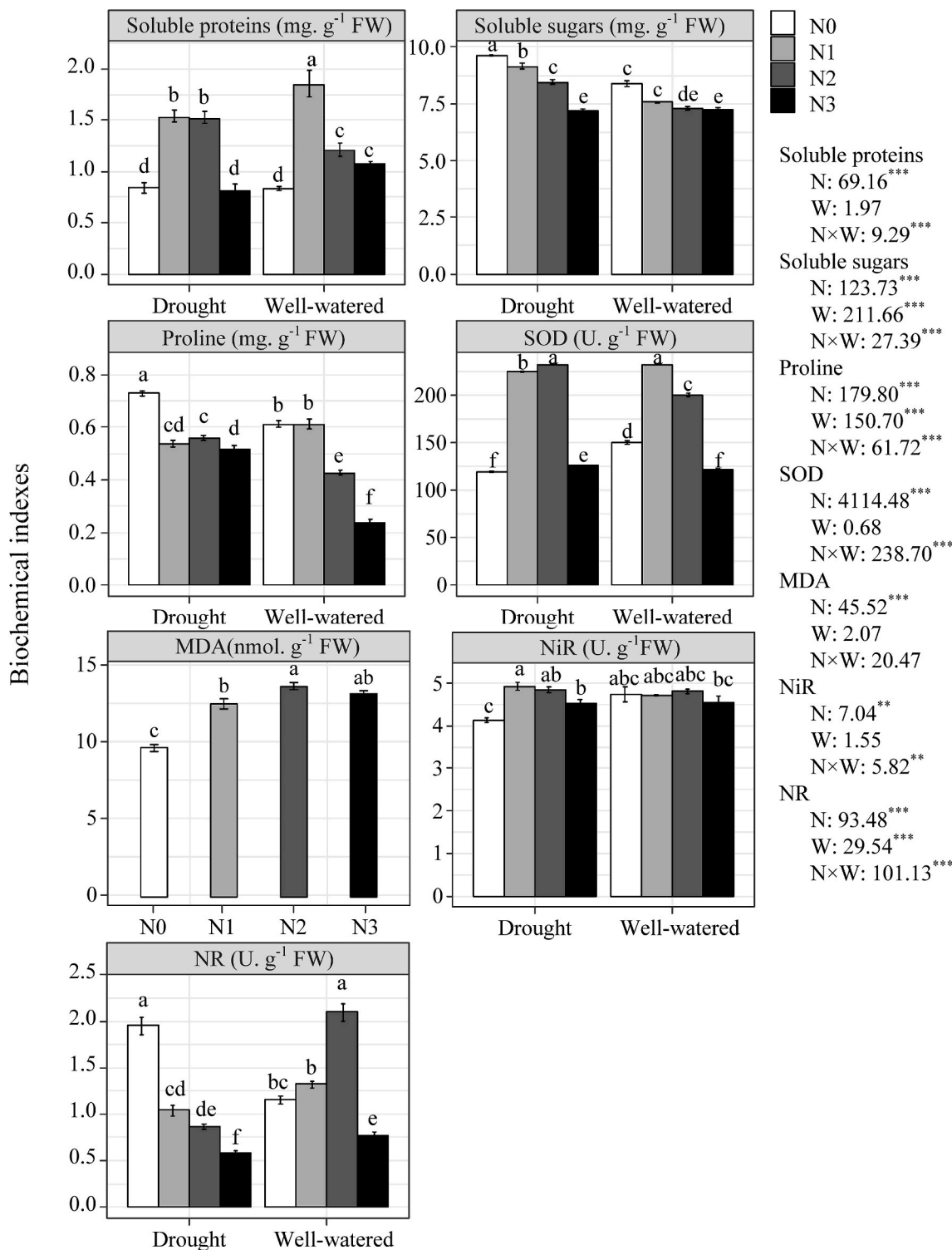
Fig. 4. Effects of nitrogen deposition (N) and water treatments (W) on antioxidant enzyme activities, N assimilation-related enzymes, osmolytes, and soluble protein contents in *Alhagi sparsifolia* seedlings leaves. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 gN.m^{-2}.yr^{-1} (N1), 6 gN.m^{-2}.yr^{-1} (N2), 9 gN.m^{-2}.yr^{-1} (N3). Values in the first part show mean ± SE (n = 3). Different letters above indicate significant differences ($P < 0.05$) according to the least significant difference (LSD) test. A summary of the results of a two-way ANOVA addressing the effects of nitrogen and water treatments is seen in the right-hand corner. *, **, ***, indicate that F value were significant at $P \leq 0.05$, 0.01, 0.001, respectively.

increased. Under simulated drought conditions, the addition of N significantly increased the distribution of N to the leaves and fine roots compared with the control group. Under the well-watered regime, the N1 group displayed significantly increased N allocation to the leaves and decreased N allocation to the fine roots. The N2 group exhibited

profoundly increased N allocation to the stems and decreased allocation to the leaves. Finally, the N3 group showed markedly reduced N allocations to the stems and fine roots and increased allocation to the coarse roots compared to the control group. The addition of N also significantly increased the relative P content at the plant level, with the exception of
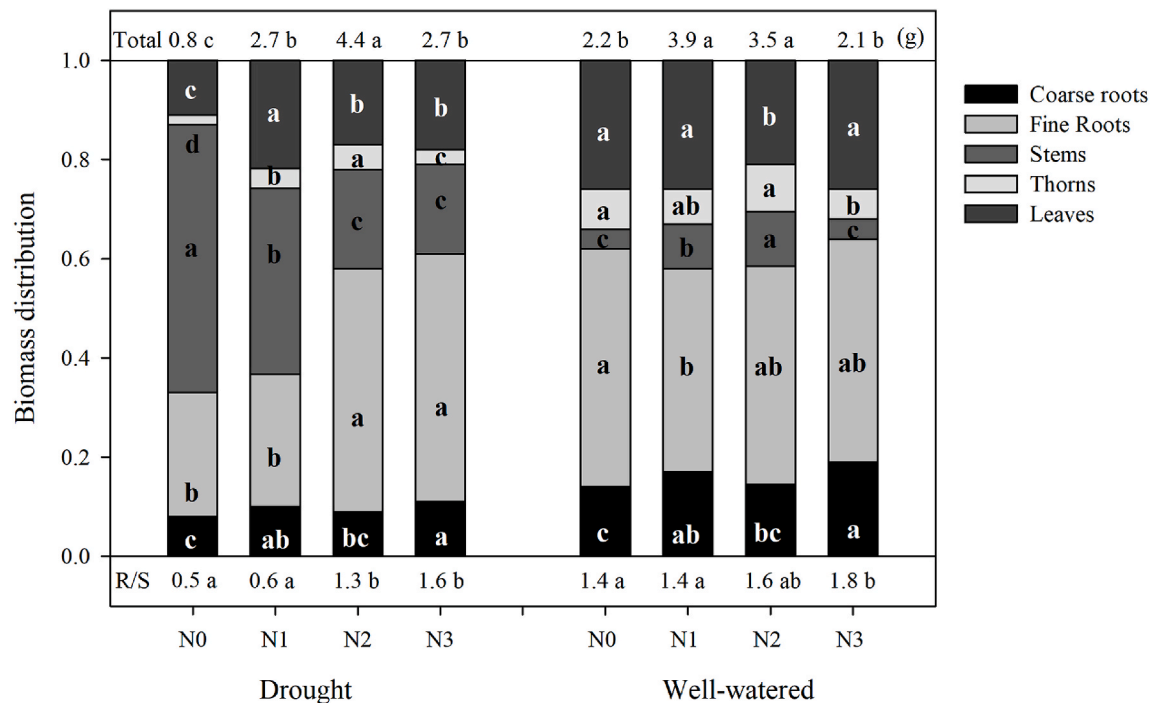
Fig. 5. Effects of nitrogen deposition (N) and water treatments (W) on biomass allocation among *Alhagi sparsifolia* seedlings organs. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 g gN.m^{-2}.yr^{-1} (N1), 6 gN.m^{-2}.yr^{-1} (N2), 9 gN.m^{-2}.yr^{-1} (N3). Bars show means ± SE (n = 3). Numbers followed by letters above bars are total biomass (g plant^{-1}) for each treatment. The numbers and letters below the bars are root biomass to shoot biomass (R/S). Different letters indicate significant differences ($P < 0.05$) among all treatments according to the least significant difference (LSD) test. A summary of the results of a two-way ANOVA addressing the effects of nitrogen and water treatments are in Supplementary information.

Table 1
Effects of nitrogen addition (N) and water treatments (W) on specific leaf area (SLA), leaf relative water content (LRWC), leaf thickness (LT), and stem base diameter (SBD) of *Alhagi sparsifolia* seedlings. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 gN.m^{-2}.yr^{-1} (N1), 6 gN.m^{-2}.yr^{-1} (N2), 9 gN.m^{-2}.yr^{-1} (N3). Values in the first part show means ± SE (n = 3). A summary of the results of a two-way ANOVA addressing the effects of nitrogen and water treatments is seen in the bottom.

Interaction				Non-interaction			
W	N	SLA (cm^2 g^{-1})	LRWC (%)	W	N	LT(mm)	SBD (mm)
Drought	N0	46.70 ± 0.89f	50.50 ± 1.06g		N0	4.33 ± 0.06c	2.12 ± 0.27b
	N1	99.37 ± 0.46e	67.09 ± 2.41ef		N1	4.60 ± 0.09b	2.77 ± 0.24a
	N2	155.29 ± 4.10a	70.25 ± 0.73de		N2	4.86 ± 0.05a	2.65 ± 0.15a
	N3	130.12 ± 1.72b	74.68 ± 0.85bc		N3	4.82 ± 0.06a	2.21 ± 0.15b
Well-watered	N0	102.73 ± 0.94de	65.77 ± 0.68f				
	N1	112.91 ± 2.63cd	71.59 ± 1.91cd	Drought			2.75 ± 0.13a
	N2	121.68 ± 3.23bc	77.16 ± 0.71 ab				
	N3	123.13 ± 8.74bc	79.64 ± 0.35a	Well-watered			2.12 ± 0.14b
F-value	N	108.16***	84.46***		N	13.27***	5.12*
	W	7.28*	77.14***		W	1.74	20.00***
	N × W	49.62***	7.77**		N × W	0.4	2.83

Means followed by different lowercase letters indicate significant differences ($P < 0.05$) among all treatments according to the least significant difference (LSD) test. *, **, ***, indicate that *F-value* were significant at $P \leq 0.05$, 0.01, 0.001, respectively.

the N3 group under the well-watered regime (Fig. 6). Under simulated drought conditions, N addition significantly increased P allocation to the leaves and decreased that to the stems. The N2 and N3 groups displayed markedly increased P allocation to the fine roots. The N3 group also exhibited improved P allocation to the coarse roots of the drought-stressed seedlings. Under the well-watered regime, no significant changes were observed in the P distribution among the leaves. The N1 and N2 groups displayed a significantly decreased P allocation to the fine roots but an increased P allocation to the stems.

The addition of N and the water regime did not affect the N:P ratios in the stems and leaves (Fig. 7). In contrast, N, water, and their combination significantly influenced the N:P ratio in the coarse roots. The N-

treated groups under simulated drought conditions and the N3 group under the well-watered regime displayed increased N:P ratios in the coarse roots. The combination of N addition and water significantly influenced the N:P ratios of the fine roots. The N1 treatment considerably improved fine root N:P ratio of drought-induced seedlings, while profoundly decreased it in well-water regime.

3.6. Relationship between traits

Although it is clear that water stress was imposed, as demonstrated by the low SWC (Table S1) and the markedly inhibited growth of the non-fertilized plants under simulated drought conditions (Figs. 5 and
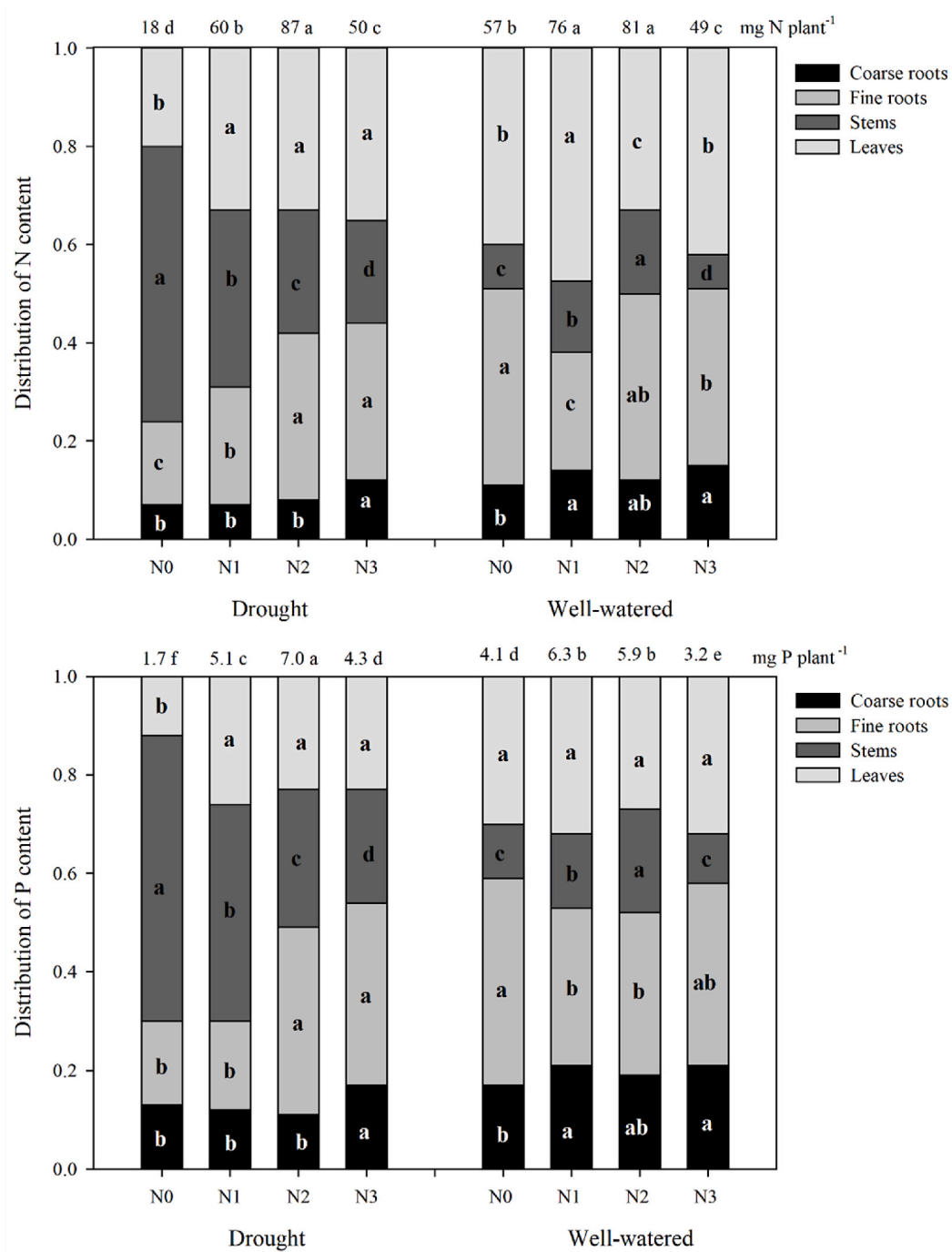
Fig. 6. Effects of nitrogen deposition (N) and water treatments (W) on nitrogen (N) and phosphorus (P) relative content in *Alhagi sparsifolia* seedlings. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 gN.m^{-2}.yr^{-1} (N1), 6 gN.m^{-2}.yr^{-1} (N2), 9 gN.m^{-2}.yr^{-1} (N3). Numbers followed by letters above bars are total N and P content (mg plant^{-1}) for each treatment. Different letters indicate significant differences ($P < 0.05$) among all treatments according to the least significant difference (LSD) test.

S1), N addition played a vital role in determining the overall growth, i. e., total biomass.

Neither the SWC values at any of the tested depths (0–20, 20–40, and 40–60 cm) nor their combinations could adequately explain the final total biomass (AIC = 80, $R^2 = 0.08$, $P = 0.66$). Therefore, we attempted to evaluate which soil traits could explain the total biomass. First, we performed multiple regression analysis considering all of the traits in Table S1 that exerted a significant influence between treatments. We selected the NO$_3^-$–N content and SWC in the three soil depths and the NH$_4^+$–N content, AN, AP, EC, and SOC values in the upper layer. The best

model (lowest AIC and highest R^2) was found to be model 1 in Table 2, which included the NO$_3^-$–N contents and SWC values at all three depths and the SOC, AP, and EC values in the upper layer. The SWC and total biomass exhibited a negative relationship, whereas all of the other variables displayed positive relationships with the total biomass. Next, we established a correlation matrix and selected the soil variables that showed a significant correlation ($P < 0.05$) with the total biomass to obtain model 2 in Table 2. The variables related to N exhibited a positive relationship with the total biomass, whereas AP, pH, and EC displayed negative relationships. The SOC and TP were excluded from this model.
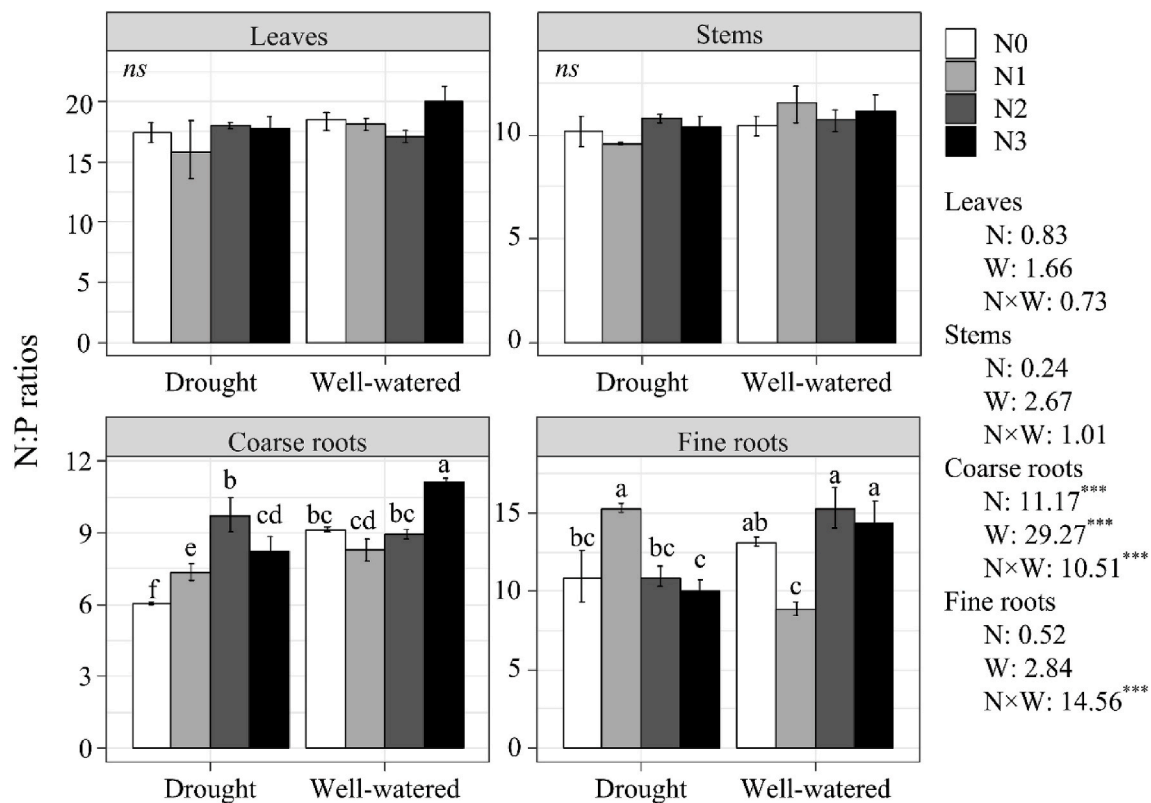
Fig. 7. Effects of nitrogen deposition (N) and water treatments (W) on nitrogen (N): phosphorus (P) ratio in *Alhagi sparsifolia* seedlings leaves. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 $gN.m^{-2}.yr^{-1}$(N1), 6 $gN.m^{-2}.yr^{-1}$ (N2), 9 $gN.m^{-2}.yr^{-1}$ (N3). Bars show means ± SD (n = 3). Different letters above indicate significant differences ($P < 0.05$) among treatments according to the least significant difference (LSD) test. A summary of the results of a two-way ANOVA addressing the effects of nitrogen and water treatments is seen in the right-hand corner of each panel. *ns* denotes no significant difference.

Then, we chose the leaf traits that were positively correlated with the total biomass and selected the optimal model (lowest AIC), which included the leaf N, SOD, and MDA values (positive relationships) and the NiR, LRWC, *E*, and SS values (negative relationships), affording model 3 in Table 2. Finally, we chose the variables related to biomass partitioning and nutrient accumulation and distribution, which were correlated with the total biomass. As represented by model 4, we found that the total biomass was positively correlated with the partitioning of biomass to the thorns and fine roots, the partitioning of N to leaves and P to stems, and higher N:P ratios in the coarse roots, and negatively correlated with the partitioning of P to the fine roots.

4. Discussion

The levels of N and water are tightly coupled to the growth of plants. Drought and infertility are the norm in the hyperarid Taklamakan Desert ecosystem (Liu et al., 2016). In this region, the drought tolerance traits of adult phreatophytes have been comprehensively studied (Arndt et al., 2004; Liu et al., 2013a). However, the adaptive responses of young phreatophyte desert seedlings to N availability and drought have received comparatively little attention. Studying the effects of N and water on desert plants could help elucidate the response of desert ecosystems to global changes.

4.1. Responses of A. sparsifolia seedlings to drought

In our study, *A. sparsifolia* seedlings displayed sensitive physiological and morphological responses to drought stress and exhibited a series of adaptive adjustments. For instance, the elevated SS and proline levels (Fig. 4) increased osmotic regulation to prevent cell membrane damage (Tariq et al., 2019). Meanwhile, the increased NR activity in conjunction

with greater allocation of nutrients and biomass to stems than to leaves and roots (Figs. S1, 4, and 5) indicate that N assimilation actively occurred in the stems, which can serve as temporary nutrient pools for future growth. The lower SLA observed for drought-stressed plants belonging to the N0 group (Table 1) indicates that in a dry environment *A. sparsifolia* seedlings tend to invest more energy in foliar defenses (particularly structural ones) (Cornelissen et al., 2003) and chemical protection such as proline and soluble sugars. However, this was at the expense of decreased productivity (total biomass, Fig. 1S). Reduced growth due to water stress has been observed in numerous other species occupying desert ecosystems (Deng et al., 2006; Zhou et al., 2011), although the reduction in R/S ratio in response to drought, in line with the theory of Poorter et al. (2012), is not common. This phenomenon will be discussed later in the context of nutrient partitioning. It is interesting to note that the simulated drought conditions did not exert a significant influence on gas exchange (Fig. 1), photosynthetic pigments (Fig. 2), soluble protein (contained larger RuBisCo) (Fig. 4), or the concentrations and ratios of N and P in leaves (Fig. 7 and Table S2). This implies that the *A. sparsifolia* seedlings were able to maintain normal photosynthetic production and homeostasis under the drought conditions. However, this appears to be inconsistent with the lower allocations of N, P, and biomass to resource-acquiring organs (i.e., leaves and fine roots) observed in the drought-stressed plants (Figs. 4–7). In combination with the lower LRWC under drought conditions, we infer that a water deficit reduces water flow from the xylem and restricts the mobility of elements from dehydrated soil, their uptake by roots, and vertical translocation toward the leaves (Gonzalez-dugo et al., 2012), which could lead to hydraulic failure and asymmetrical changes in nutrient partitioning between different organs.

Table 2
Relationship between total biomass (g) and physic-chemical soil traits.

Model	AIC	R^2	Number of variables tested	Variables excluded	Total biomass =
Soil traits					
Model 1	3.8	0.98	11	NH_4^+-$N_{(0-20)}$, $AN_{(0-20)}$	$1.01 + 0.14$ NO_3^-–$N_{(0-20)} + 0.03$ NO_3^--$N_{(20-40)} + 0.05$ NO_3^--$N_{(40-60)} + 0.36$ $AP_{(0-20)}$ - 0.40 $SOC_{(0-20)}$ - 0.01 $EC_{(0-20)}$ - 5.47 $SWC_{(0-20)}$ - 3.21 $SWC_{(20-40)}$ - 2.46 $SWC_{(40-60)}$
Model 2	19.7	0.95	9	$SOC_{(40-60)}$, $P_{(40-60)}$	$5.21 + 6.10$ $TN_{(0-20)} + 0.11$ NH_4^+-$N_{(20-40)} + 0.10$ NO_3^--$N_{(0-20)} + 0.07$ NO_3^--$N_{(40-60)} - 0.54$ $AP_{(20-40)} -0.99$ $pH_{(20-40)}$-0.04 $EC_{(0-20)}$
Leaf traits					
Model 3	2.34	0.98	12	SP, P_n, LT, F_v/F_m	$2.65 + 0.02$ SOD + 0.01 SLA + 0.2 MDA + 0.09 leaf N – 0.55 NiR – 4.07 LRWC – 0.2 E - 0.55 SS
Biomass partitioning and nutrient distribution traits					
Model 4	44.58	0.78	11	R/S, stem: total BM, leaf: total P content, stem: total N content	$-16.19 + 1.25$ SBD + 14.23 thorn: total BM + 22.6 fine root: total BM + 11.0 leaf: total N content + 13.0 stem: total P content + 0.25 coarse roots N:P– 11.3 fine root: total P content

Abbreviations: AIC, Akaike Information Criterion; AN, available N; AP, available P; EC, electrical conductivity; SWC, soil water content; TN, total N; BM, biomass; SLA, specific leaf area; LRWC, leaf relative water content; LT, leaf thickness; SBD, stem base diameter; SP, soluble proteins; SS, soluble sugars.

4.2. Role of N in modulating the drought resistance of A. sparsifolia seedlings

Numerous researchers have demonstrated that increased N availability can improve the WUE (Zhao et al., 2019; Zhou et al., 2011), reflecting the coupled relationship between N and water. However, in this study, only low levels of N addition (N1) improved the WUE of the seedlings, while the water regime did not display any influence on the WUE (Fig. 1). N addition significantly increased or maintained the P_n, g_s, E, and F_v/F_m values (Figs. 1 and 3) while increasing the levels of soluble proteins, SOD, and MDA (Fig. 4), suggesting that moderate N addition could improve the photosynthetic process and modulate drought stress to a certain degree. Furthermore, the improved SLA (Table 1) upon N addition may imply that the N-treated plants exhibited a higher relative growth rate (Wellstein et al., 2017). The increased leaf thickness (Table 1) upon N addition also indicated increased tolerance to drought, perhaps by allowing plants to allocate additional biomass to the leaves to deal with drought stress (Niinemets, 2001; Witkowski and Lamont, 1991). Moreover, N addition significantly increased or maintained biomass among the various plant organs in comparison to their non-fertilized counterparts (Fig. S1). The reduced SS contents in the treatment groups (Fig. 4) suggest that N addition may improve the

conversion of soluble sugars to starch or structural carbohydrates. In addition, the increased allocation of biomass and nutrients to resource-acquiring organs (i.e., leaves and fine roots) mediated by N addition in drought-stressed plants (Figs. 5 and 6) indicates that N addition improved the ability to take up and assimilate N. However, we found that the addition of high levels of N reduced the levels of SS, proline, and NR in the *A. sparsifolia* seedlings (Fig. 4), indicating that excessive N deposition exerted a negative influence on the chemical defense of the seedlings. Thus, their future growth may be restricted by other constraints.

4.3. N addition affects the acclimation of A. sparsifolia seedlings via nutrient allocation and N:P stoichiometry

The appropriate allocation of limited resources is a prerequisite for plants to adapt to changes in their environment. N is an integral component of enzymes, while P is a crucial constituent of nucleic acids and membrane lipids (Elser et al., 2000). The availability of N and P to plants is a critical determinant of the productivity and C sink of an ecosystem, especially under future conditions of N deposition and global climate change (Ågren et al., 2012; Wieder et al., 2015). Leaves, woody stems, and roots play distinct roles in ecosystem function. Foliar N and P are critical for metabolism, whereas woody stems provide storage for these elements, which are essential for plant respiration and internal nutrient recycling (Heineman et al., 2016; Yan et al., 2016). To meet the demands of growth, plants must allocate biomass and nutrients between woody stems, roots, and leaves (Yang et al., 2014). The concentrations and control of nutrients within roots and stems remain poorly understood in comparison to leaves, despite the fact that the former organs account for the majority of biomass and nutrients in plants (Kleyer and Minden, 2015), especially in desert species. In this study, it is interesting to note that the organ distributions of N and P were quite different between plants under simulated drought and well-watered conditions (Fig. 6). The drought-stressed plants in the N0 group accumulated higher amounts of N and P in the stems, while the addition of small amounts of N (N1) reduced the allocation of these two nutrients to the stems and improved that to the leaves. Furthermore, the addition of large amounts of N (N3) markedly increased the allocation of nutrients to the fine roots. In contrast, N addition did not afford a clear change in the organ distributions of N and P for the well-watered plants (Fig. 6). The accumulation of N and P in the stems of drought-stressed plants in soils with low N availability indicates that as N becomes more limited under drought conditions, plants accumulate the small quantities of N and P that they can take up in the stems as reserves for future growth. As the N deficiency was replenished, greater growth was observed even under drought conditions, which even reached the levels of that in the well-watered plants. Thus, water may limit plant growth via N and P starvation more than the lack of water itself, as the drought-stressed plants achieved a similar size as the well-watered plants upon N addition to the soil (Fig. 5).

The N:P stoichiometry of plant tissues may reflect vital biochemical constraints on the relative investments into proteins (which are particularly rich in N) or ribosomal RNA (a metabolically important sink for P). The foliar N:P ratio has been widely applied as an indicator of soil nutrient limitation for herbaceous and woody species (Koerselman and Meuleman, 1996). Our results (Fig. 7 and Table S2) revealed that foliar P limitations (N:P ratio > 16) occurred in all of the treatment groups, according to the theory of Koerselman and Meuleman (1996). This implies that P limitation is widely ingrained in desert ecosystems owing to the low precipitation and high evaporation (Yang et al., 2014). Compared with the leaves, the N:P ratios of the stems and coarse roots were lower (N:P ratio <14), indicating varying sensitivities among organs to soil nutrients under N addition and water regimes and that the stems and coarse roots act as nutrient reservoirs during active growth to maintain healthy plant growth. Consequently, Schreeg et al. (2014) proposed that the N:P ratios of stems and roots (coarse roots and fine

roots were not distinguished in this study) were more sensitive indicators of soil nutrient availability than expanded leaves (the most commonly sampled tissue). Differentiation of the fine and coarse roots is crucial for obtaining a comprehensive understanding, because the two types of root tissue perform distinct functions (Wang et al., 2017). As a starting point for the flow of nutrients and water from the soil to other plant tissues, fine roots can sense changes in the availability of soil resources more rapidly than foliage, especially for phreatophytes in infertile ecosystems. Therefore, the nutrient elements in roots, and especially those in fine roots, are more responsive to changes in soil nutrient availability than foliage (Kou et al., 2018; Schachtman and Goodger, 2008; Walter and Schurr, 2005). While fine roots are the main organ for water and nutrient uptake, coarse roots are the main organ for water transport. Again, the N:P ratio in the fine roots may be a more refined indicator of soil nutrient status because this organ is less dependent on maintaining an optimal ratio and is highly metabolically active, requiring a substantial allocation of N and P for the synthesis of the carrier enzymes that actively take up nutrients from the soil (Garrish et al., 2010; Schreeg et al., 2014; Wang et al., 2017). However, this must be verified by further research. In our study, the N:P ratio in the fine roots was only affected by the combination of N addition and drought stress (Table S3). The addition of low amounts of N increased the N:P ratio in the fine roots to 14–16 under simulated drought conditions, implying that N addition could induce N and P starvation (co-limitation) in drought-stressed seedlings.

4.4. Eco-physiological acclimation guarantees higher biomass accumulation of A. sparsifolia seedlings in desert environments

The *A. sparsifolia* seedlings were found to allocate more of their biomass to the fine roots than to the coarse roots for all treatment groups, indicating that the limiting factor for growth was belowground from an optimal partitioning perspective (Gedroc et al., 1996). Under well-watered conditions, the N1 group displayed a decreased fine root mass fraction and an increased stem mass fraction compared to the control group, implying that low-level N addition relieved belowground nutrient limitation, whereas the N2 and N3 groups, which had a greater requirement for water, exhibited an increased fine root mass fraction after receiving sufficient N and P supply. Under drought conditions, N addition increased the biomass allocation to the fine roots, which could take up sufficient N, P, and water (Fig. 6 and Table 1). Consequently, biomass accumulation in the drought-stressed plants upon N addition was as high as that under well-watered conditions. This reflects the concept that the biomass accumulation of a species adapted to desert conditions cannot be predicted solely on the basis of soil water content, as numerous morphological and physiological acclimations also play a role. Biomass accumulation was higher in soils with greater NO_3^-–N availability in the bottom soil (40–60 cm) and higher available P levels in the topsoil (0–20 cm). Furthermore, higher SWC and EC values in the topsoil led to higher biomass accumulation (model 1 in Table 2). However, it is very interesting to note that the SWC was not included in the model to explain total biomass, as there was no correlation between the SWC and growth. The N and P concentrations in the soil were more suitable for explaining biomass accumulation than the SWC (model 2 in Table 2). This finding was significant because it was hypothesized that desert plants survive in dry soils. After all, they use groundwater to avoid a water deficit (Arndt et al., 2004; Cheng et al., 2019). However, the results of this study demonstrate that the seedlings possessed numerous strategies to tolerate drought, and the changes at the leaf level reflected their acclimation and were related to higher biomass accumulation. The capacity of *A. sparsifolia* to develop leaves with higher values of SLA, SOD activity, and MDA and N concentrations was related to higher biomass accumulation. On the other hand, leaves with lower NiR activity, LRWC, *E*, and SS content were linked to higher biomass accumulation (model 3 in Table 2). Again, it was apparent that soil water availability was not the main factor inhibiting growth, and plants

can partially close their stomata and tolerate partial leaf dehydration with no penalty in terms of biomass accumulation. Finally, as necessary in leaf physiology was the partitioning of biomass and nutrients among the organs. The allocation of biomass to the stems, thorns, and fine roots was essential to increase the total biomass accumulation. This biomass partitioning enabled plants to take up N, which was preferentially allocated to the leaves and coarse roots, and P, which was preferentially allocated to stems and not to fine roots (model 4 in Table 2).

5. Conclusions

The addition of N and simulated drought conditions significantly influenced photosynthesis, drought tolerance characteristics, morphological traits, biomass allocation strategy, and nutrient distribution patterns among the various organs of *A. sparsifolia*. We have demonstrated that *A. sparsifolia* possesses numerous strategies for tolerating drought, including morphological and physiological changes. The addition of N was crucial for enhancing plant growth under drought conditions, which was predominantly attributable to its positive impact on N and P uptake capacity mediated by increased allocation of biomass to the roots. The N:P ratio in fine roots may be a more refined indicator of soil nutrient status in hyperarid desert ecosystems. Our results are anticipated to facilitate a greater understanding of the morphological and physiological plasticity of young phreatophyte desert seedlings and their responses to N deposition and drought in the desert–oasis ecotone of northwestern China.

CRediT authorship contribution statement

Zhihao Zhang: Investigation, Methodology, Formal analysis, Writing - original draft. **Akash Tariq:** Conceptualization, Methodology, Formal analysis, Writing - review & editing, Supervision. **Fanjiang Zeng:** Conceptualization, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Corina Graciano:** Conceptualization, Formal analysis, Writing - review & editing. **Bo Zhang:** Investigation, Resources, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.plaphy.2020.08.036.

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