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The Physiological Adjustments of Two Xerophytic Shrubs to Long-Term Summer Drought

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Abstract: Adaptive characteristics of plants, such as those associated with photosynthesis and resource use efficiency, are usually affected by synthesis costs and resource availability. The impact of extreme climate events such as long-term drought on plant physiological functions needs to be examined, particularly as it concerns the internal management of water and nitrogen (N) resources. In this study, we evaluated the resource management strategies for water and N by xerophytic shrubs, *Artemisia ordosica* and *Salix psammophila*, under extreme summer drought. This was carried out by comparing the plants' physiological status during periods of wet and dry summer conditions in 2019 and 2021. Compared with the wet period, *A. ordosica* and *S. psammophila* both decreased their light-saturated net carbon (C) assimilation rate (A_{sat}), stomatal conductance (g_s), transpiration rate (E), leaf N content per leaf area (N_{area}), and photosynthetic N use efficiency (PNUE) during the summer drought. Whether in wet or dry summers, the gas-exchange parameters and PNUE of *A. ordosica* were generally greater than those associated with *S. psammophila*. The instantaneous water use efficiency (IWUE) response to drought varied with species. As a drought-tolerant species, the *A. ordosica* shrubs increased their IWUE during drought, whereas the *S. psammophila* shrubs (less drought-tolerant) decreased theirs. The divergent responses to drought by the two species were largely related to differences in the sensitivity of g_s, and as a result, E. Compared with *A. ordosica*, *S. psammophila*'s inferior plasticity regarding g_s response affected its ability to conserve water during drought. Our research illustrates the need for assessing plasticity in g_s when addressing plant adaptation to long-term drought. A high dry-season IWUE in xerophytic shrubs can benefit the plants by augmenting their C gain.

Keywords: adaptive plant traits; photosynthesis; resource use efficiencies and availability; seasonal variation; summer drought; synthesis costs

1. Introduction

Drylands cover around 40% of the earth's continental area and support more than 38% of the world's population [1]. Some studies have shown that drought stress may exacerbate the widespread death of plants worldwide, especially in arid and semiarid regions, and drought stress is considered one of the most destructive abiotic stresses on plant survival [2,3]. It is estimated that in the future, many regions around the world

will experience more severe and widespread droughts, which will lead to increasingly fierce competition among plants for water resources [4]. Understanding the physiological adaptation mechanisms of woody plants to extreme drought has emerged as a key focus in ecology and plant science.

Plant resource use efficiencies (RUEs) are key response variables that reflect the physiological status of terrestrial ecosystems. Measures of RUEs have been widely used to understand ecosystem responses to climate change and extreme weather events [5–7]. At the leaf scale, plant carbon (C) assimilation largely depends on the availability of photosynthetic resources, such as light, water, and nitrogen (N). Strong climatic fluctuations (e.g., seasonal drought) have been shown to change resource supply [3,8,9], which can affect plant resource accommodation over several timescales [6,10]. In drylands, how plants make use of natural resources and maximize their leaf C gains are essential to plant survival.

In environments where light is not a limiting resource, such as in shrublands and grasslands [11,12], water and available soil nutrients, particularly N, are viewed as the main constraints on plant C fixation in drylands [13–15]. Instantaneous water use efficiency (IWUE), defined as the ratio of plant net photosynthesis to transpiration, reflects the interaction between C gains and water consumption [16,17]. Most plant N is invested in photosynthesis. The variation in photosynthetic N use efficiency (PNUE, i.e., the ratio of net photosynthesis to leaf N content) reflects the change in plant C assimilation [18–20]. These two RUEs are widely viewed as ecological indicators of plant drought tolerance [21–23].

Plant economic theory projects that plants prefer to maximize their use efficiencies of the most limiting resources to offset constraints on C uptake [24,25]. Meanwhile, C gain by plants from resource use declines as the supply of the resource increases [26,27]. Sometimes, a mutual coupling is established between different RUEs [6,22]. Increases in water supply can lead to increases in the PNUE and decreases in the IWUE [28]. Instantaneous water use efficiency can also increase when water supplies are low and nutrient supplies are high [29]. In this context, dryland-adapted plants during short summer droughts can extract soil water resources and reduce the investment in photosynthetic N. Water–N tradeoffs between resource acquisition seem to conform with the stress response of plants to water losses [30]. During dry summer conditions in oak–grass dominated savanna, improving the IWUE by *Quercus douglasii* comes at a cost by decreasing the PNUE [31]. An improved IWUE during drought increases drought tolerance [21,32]. Although plants sacrifice their partial C gain during a drought, any C loss during this time can be counterbalanced later during a consecutive wet season [6,9].

However, the exact effects of extreme drought on leaf-level photosynthesis in mature foliage are greatly debated, especially in terms of the IWUE. For instance, trees in the Amazonian basin and common apple trees significantly reduce their C assimilation rates during long-term drought but increase their IWUE [4,33]. By comparison, the IWUE in *Pinus ponderosa* tends to decrease with strong diffusion disruptions under extended drought [34]. *Erica multiflora*, in contrast, will modify its water use strategy depending on the severity of the drought. *E. multiflora* is known to increase its IWUE to reduce water losses during mild drought and decrease its IWUE during severe drought [9]. These studies have emphasized that there is not always a single suite of tradeoffs between use efficiencies of constraining and non-constraining resources [12,23]. Together, the impact of long-term drought on RUEs may be very different than what would be recorded over the short term.

In northwest China, the temperate semiarid climate of the region is extremely variable, commonly characterized by its very cold winters and hot summers. The precipitation during summer is featured as infrequent and irregularly distributed, and it is inconsistent from year to year [35,36]. A typical summer drought is usually accompanied by very high air temperatures, excessive global solar radiation, and low soil water content. These conditions typically persist for several months at a time, causing significant problems for plant growth and survival [2]. Just how local shrubs adjust their internal water and N budgets to adapt to extreme drought remains uncertain.

Artemisia ordosica and *Salix psammophila* are two common shrub species found growing in the semiarid areas of the Mu Us Desert [37]. *A. ordosica* is a slow-growing shrub with short needle-shaped leaves, commonly reaching a height of about 0.5 m. Its main root extends to about 0.5 m. In contrast, *S. psammophila* has narrow leaves and a relatively open canopy. Mature plants can reach a height of between 2–3 m. The plant has an abundance of horizontally distributed roots [38,39]. Leaf phenology in *A. ordosica* and *S. psammophila* is about the same, with leaf development from April until May, and in September, there is the onset of leaf senescence. As the dominant shrubs in the area, resource competition between these two species has drawn much attention [36,38,40].

Previous studies have suggested that *A. ordosica* can assimilate more C than *S. psammophila* through improved photosynthetic performance and high PSII photochemical efficiency during short-term drought [12,41,42]. However, it is unclear whether long-term drought can further limit water and N budgets in xerophytic plants and change their interactions. This increases the uncertainty in the prediction of shrubland productivity in response to extreme weather events [43]. We hypothesize that (i) *A. ordosica* maintains higher rates of photosynthesis during severe drought by the efficient use of water resources and that (ii) the increase in the IWUE in xerophytic shrubs during long-term drought may be attributed to decreased stomatal conductance. Our main objectives of the study were to (i) examine the physiological plasticity of two xerophytic shrubs exposed to long-term summer drought and (ii) elucidate the mechanisms by which water and N budgets in the shrubs are affected by long-term water shortages.

2. Materials and Methods

2.1. Site Description

This study was conducted at the Yanchi Research Station near the southern edge of the Mu Us Desert, northwest China (37°42′31″ N, 107°13′47″ E, 1530 m above mean sea level, a.s.l.). The climate is mid-temperate, semiarid continental with a mean annual air temperature of 8.3 °C and precipitation (MAP) of 292 mm; the meteorological data were derived from a local weather station about 20 km from the research station. Precipitation shows large seasonal (~80% falling during June–September) and inter-annual variations (145–587 mm for the period 1954–2004) [44]. The soil is an Arenosol (the FAO-UNESCO soil classification) with a total nitrogen content of 0.1–0.2 g kg^{-1} and a soil organic carbon (C) content of about 2.0 g kg^{-1} [45].

The shrubland community is dominated by a mixture of xerophytic shrub species, including *A. ordosica*, *Hedysarum mongolicum*, *S. psammophila*, and *Hedysarum scoparium*, with mean area coverage of 35, 30, 15, and 5%, respectively. A minor grass component accounts for about 15% of the ground coverage, involving a mixture of *Leymus secalinus*, *Stipa glareosa*, and *Pennisetum centrasiaticum*. All plants grow naturally without human interference. The upper soil (i.e., 0–30 cm) water supply is entirely derived from precipitation, as the water table lies well below 8 m below ground.

2.2. Gas-Exchange Measurements

The long-term observation plot (20 m × 30 m) was located on a fixed sand dune on the western side of the Yanchi Research Station. The terrain of the plot was characterized by its flat topography, with slopes measuring less than 10° [46]. The dominant shrub species within this plot were *A. ordosica* and *S. psammophila*, with an average age of 17 years [47]. Gas exchange measurements were conducted on three randomly established 5 m × 5 m plots in the experimental plot. Three individuals each of both *A. ordosica* and *S. psammophila* with similar growth and no pests or diseases were selected in each plot as biological repetitions (n = 9). The growth information of the individual plants is shown in Table 1.

Table 1. Growth characteristics of monitored sample plants of *Artemisia ordosica* and *Salix psammophila* in 2021. Bracketed values are standard error of estimate (SE, n = 9).

Variables	Species	
	A. ordosica	*S. psammophila*
Crown diameter (cm $\times$ cm)	115 $\times$ 105	127 $\times$ 112
Maximum height (cm)	57 (5)	222 (13)
Canopy coverage (%)	82 (5)	93 (3)
Aboveground biomass (g m^{-2})	433 (32)	2910 (78)

Leaf gas exchange measurements were acquired in situ on fully expanded leaves of *A. ordosica* and *S. psammophila*, using a portable gas exchange analyzer (LI-6400; Li-Cor Inc., Lincoln, NE, USA) equipped with a chamber with red and blue LED light sources (6400-02B; Li-Cor Inc., Lincoln, NE, USA). The measurements were conducted every ten days from June until August in 2019 and 2021. A cluster of sunlit leaves in the upper canopy of each individual were measured between 8:00 and 10:00 am (Standard Beijing Time, UTC+8 h, before the stomata closed at noon) on near-cloud-free, sunny days. Before making measurements, the leaves were acclimated in the chamber for 15–20 min at a temperature of 25 °C, relative humidity of 50–70%, CO_2 concentration of 400 parts per million by volume (ppm), and a light-saturated photosynthetic photon flux density (PPFD) of 1800 µmol m^{-2} s^{-1} (based on the results of light response curves, Figure S1) until the net C assimilation rate (A_n) stabilized [42,43]. Then, the light-saturated net C assimilation rate (A_{sat}), stomatal conductance (g_s), and transpiration rate (E) were recorded; the IWUE was calculated as the ratio of A_{sat} to E.

2.3. Specific Leaf Area and N Concentration

Owing to the fact that the leaf areas of *A. ordosica* and *S. psammophila* are very small, a cluster of leaves measured by gas exchange cannot directly measure leaf traits (e.g., leaf nitrogen concentration). Following the gas exchange measurements, leaf samples were excised from neighboring shrubs (n = 9) with characteristics similar to the shrubs used in the gas exchange measurements to assess the leaf area, dry weight, and N concentration of the foliage [12,43]. The leaf area was computed from photographs of the sampled foliage using the ImageJ software version_v1.8.0 [48]. Each leaf was subsequently oven-dried for 72 h at 65 °C and weighed to facilitate the calculation of the leaf dry mass per leaf area (LMA). The leaf N concentration (LNC) was determined with an elemental analyzer (Vario Max CN Element Analyzer, Elementar, LSB, Langenselbold, Germany). The nitrogen content per leaf area (i.e., N_{area}) was estimated from the LNC and LMA, with the PNUE being specified as the ratio of A_{sat} to N_{area}.

2.4. Hydrometeorological Measurements

Environmental factors were measured at the same time that the gas exchange measurements were acquired. Air temperature (T_a) and relative humidity (RH) were measured with a humidity and temperature probe (HMP155 A, Vaisala, Helsinki, Finland), while photosynthetically active radiation (PAR) was measured with a quantum flux sensor (PAR-LITE, Kipp & Zonen, Delft, The Netherlands), both mounted on a 6 m tall eddy-covariance (EC) tower located nearby (about 100 m). Precipitation (PPT) was assessed by a tipping-bucket rain gauge (TE525WS, Campbell Scientific Inc., Logan, UT, USA) installed in an opening adjacent to the EC tower. The volumetric soil water content near the tower was measured at two soil depths (i.e., at 10 and 30 cm depths), with each depth having three replicate sensors installed (i.e., ECH2O-5TE, Decagon Devices, Pullman, WA, USA). In this study, we only considered the effect of the soil volumetric water content at a 30 cm depth on the photosynthesis of *Artemisia ordosica* and *Salix psammophila* due to the fact that the main root systems of two species are usually distributed at about a 30 cm soil depth [42].

2.5. Data Analysis

The data were checked for normality (by means of the Kolmogorov–Smirnov test) and homogeneity of variance (Levene's test). For all variables, the data were analyzed by two-way ANOVA, with season and species as the main fixed factors plus a season × species interaction term. Linear regression was used to determine the relationship between the PNUE, IWUE, and related biophysical factors. Slopes of linear regression were used to denote the sensitivity of the RUEs to the various biophysical factors. Testing of the differences in the slopes between species or years was accomplished with the *diffslope* option in the *Simba* R-library. All statistical analyses were performed using the R platform version 3.6.3 (The R Development Core Team) and SPSS version 25.0 (SPSS Inc., Chicago, IL, USA). The critical *p*-value denoting statistical significance was set at 0.05.

3. Results

3.1. Seasonal Changes in Environmental Factors

According to the meteorological data from the local weather station over the past 60 years (i.e., from 1962–2021), we compared the shrubs' responses during a wet summer in 2019 against their responses during an unusually dry summer in 2021 (Figures 1 and 2). The total precipitation (PPT) during the summer of 2019 was 189 mm, which was 27% greater than the 1962–2021 mean. During this time, the volumetric soil water content (VWC) remained high, ranging from 0.066–0.16 $m^3 m^{-3}$ during the entire summer, with a mean value of 0.10 $m^3 m^{-3}$ (Figure 2).
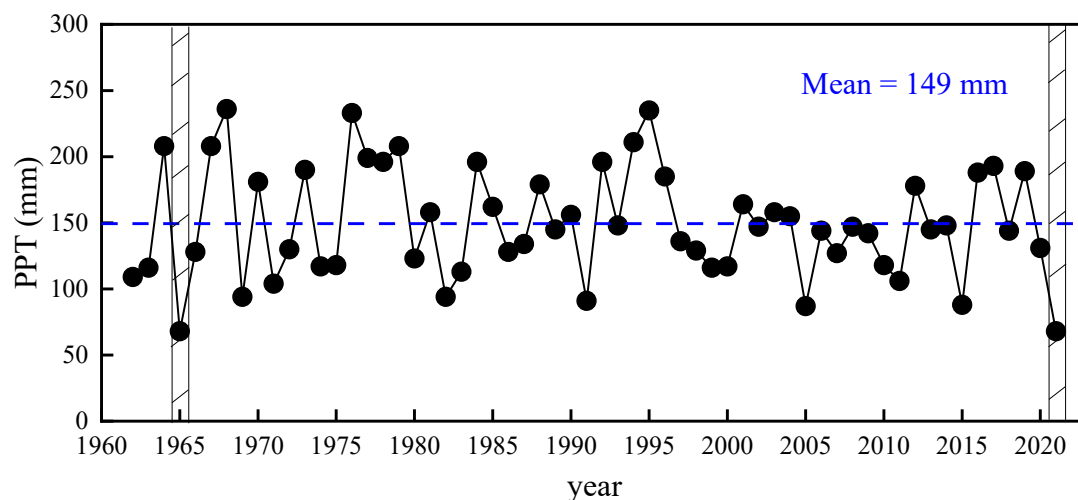

Figure 1. Interannual variation in annual total precipitation (PPT) during the June–August period of 1962–2021. The cross-hatched vertical areas show the years with the driest summers (1965 and 2021) during the past 60 years (1962–2021).

By contrast, during the unusually dry summer of 2021 (i.e., June–August), the PPT was the lowest (68 mm) over the 60-year period (except for 1965), which was about 54 and 64% lower than the 60-year and 2019 means, respectively. The soil water content during the summer of 2021 remained low, ranging from 0.059–0.082 $m^3 m^{-3}$ (Figure 2), and the mean VWC decreased by about 35% relative to the 2019 mean.

Moreover, the mean air temperature (T_a) was 1.8 °C greater than the 2019 mean, and the mean water vapor pressure deficit (VPD) was 49% greater than the 2019 mean (Figure 2). Especially in July, the mean T_a was 3.7 °C greater than the 2019 mean, and the mean VPD was 61% greater than the 2019 mean. Although both shrub species experienced severe drought during the summer of 2021, no widespread leaf discoloration (i.e., progressive color change from green to yellow) or shedding was observed.
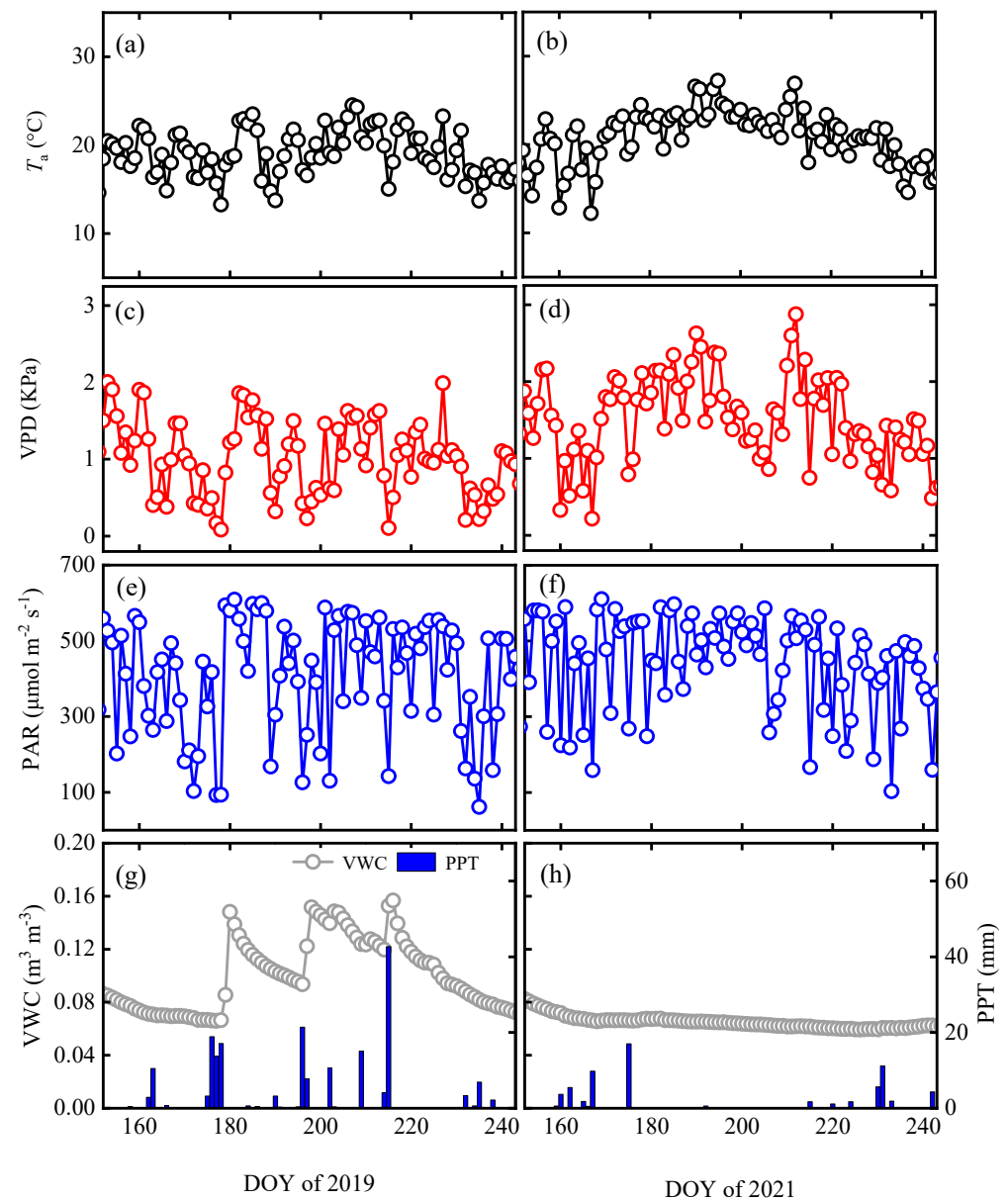
Figure 2. Seasonal variation in daily mean air temperatures (T_a, (**a**,**b**)), water vapor pressure deficit (VPD, (**c**,**d**)), photosynthetically active radiation (PAR, (**e**,**f**)), and volumetric soil water content at a 30 cm depth (VWC, (**g**,**h**)) during the summer (i.e., June–August) of 2019 and 2021, respectively.

3.2. Seasonal Changes in A_{sat}, g_s, and E

The parameters A_{sat}, g_s, and E for both species gradually increased over time during the wet summer (Figure 3a–f). The photosynthetic performance of *A. ordosica* peaked in early August, and the peak date of *S. psammophila* was about 20 days behind that of *A. ordosica*. Better photosynthesis was observed during the wet summer in *A. ordosica*. The mean A_{sat}, g_s, and E in *S. psammophila* were significantly lower (by 60.9, 63.3, and 62.2%, respectively) than the same values in *A. ordosica* during the wet summer (Figure 3a–f). Relative to the wet summer, the dry summer had significant declines in photosynthesis in both species, leading to a variable impact on the two species (Figure 3a–f). All the gas exchange parameters declined from early July until early August (DOY 183–213), maintaining low levels until the end of the study period. The mean A_{sat}, g_s, and E in *S. psammophila* were significantly lower at about 68.2, 61.5, and 44.1%, respectively, of the equivalent values in *A. ordosica* during the dry summer (Table 2). There were significant interactions between season and species for g_s and E (Table 2).
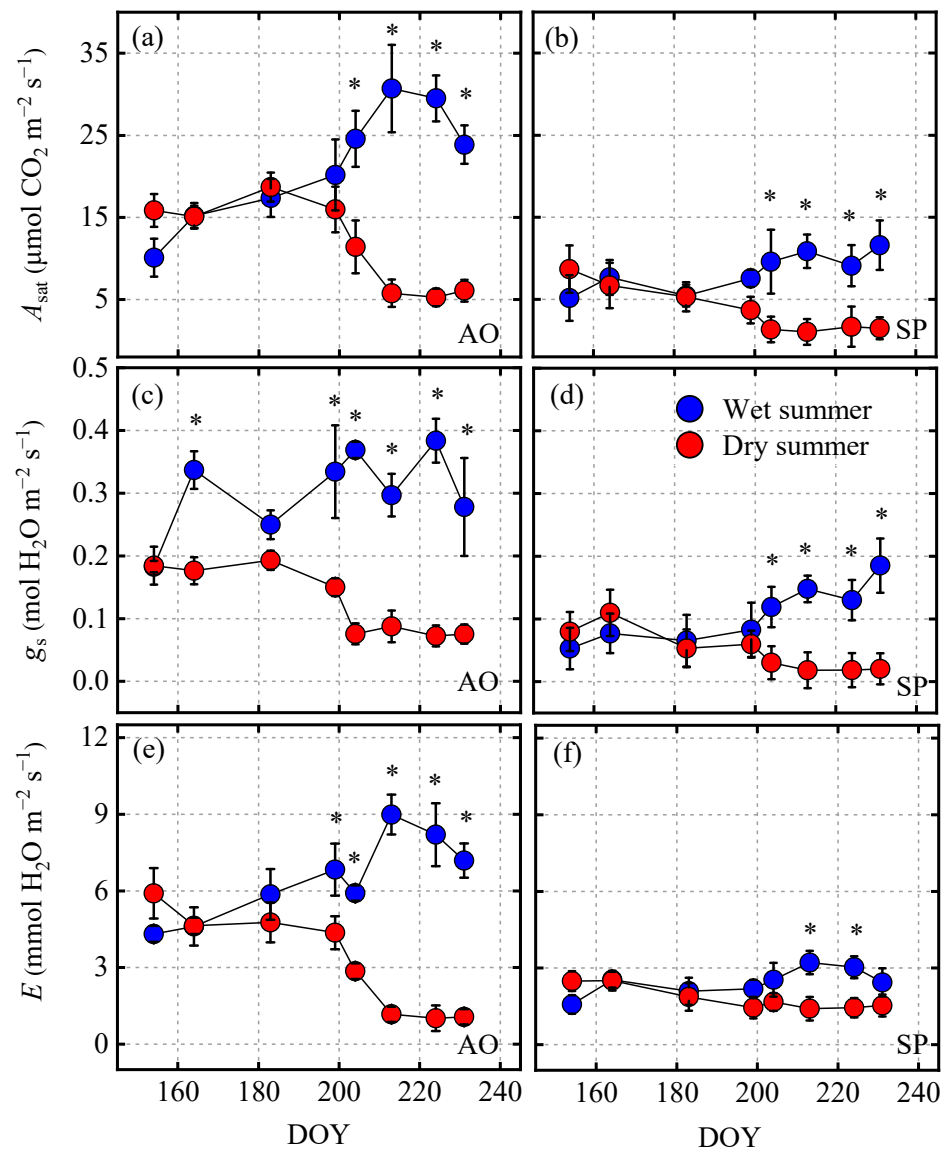
Figure 3. Seasonal difference in light-saturated net C assimilation rate (A_{sat}, (**a**,**b**)), stomatal conductance (g_s, (**c**,**d**)), and transpiration rate (E, (**e**,**f**)) in *A. ordosica* (AO, left-side panels) and *S. psammophila* (SP, right-side panels), respectively. Error bars represent standard error. Asterisks represent significant differences in each measurement point on the same DOY between wet and dry summers ($p < 0.05$).

Table 2. Two-way ANOVA results of the effect of season, species, and season × species on plant parameters.

Variables	Season		Species		Season × Species	
	F	**p**	**F**	**p**	**F**	**p**
A_{sat}	17.56	<0.0001	38.15	<0.0001	2.17	0.15
g_s	42.17	<0.0001	57.17	<0.0001	10.62	<0.01
E	17.61	<0.001	34.16	<0.001	7.81	<0.05
IWUE	0.98	0.33	12.11	<0.01	15.89	<0.0001
PNUE	15.40	<0.001	35.59	<0.0001	0.69	0.41
LMA	2.03	0.09	22.73	<0.0001	0.53	0.47
N_{area}	14.51	<0.001	20.09	<0.0001	0.21	0.65

3.3. Seasonal Changes in LMA and N_{area}

The seasonal LMA values associated with *A. ordosica* and *S. psammophila* during the wet summer usually reached their maxima in early June (121.0 vs. 106.6 g m^{-2}, respectively) and subsequently decreasing during the rest of June, stabilizing from July–August (Figure 4a,b). The leaf mass per leaf area in *A. ordosica* showed higher seasonal variability than the LMA in *S. psammophila* (Figure 4a,b). The mean LMA in the two shrub species did not differ between the two summers. Irrespective of wet or dry conditions, the mean LMA associated with *A. ordosica* was appreciably greater than the LMA in *S. psammophila* (Figure 4; Table 2).
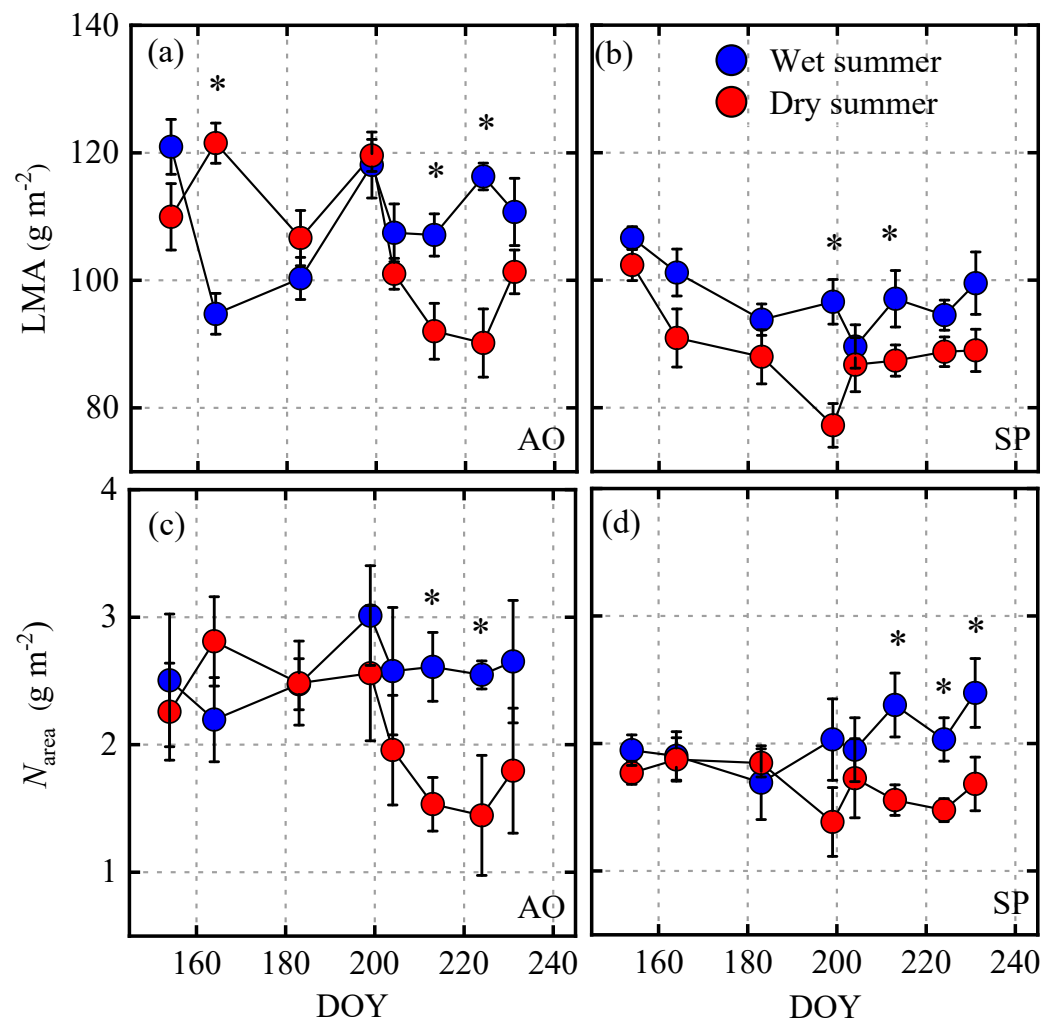
Figure 4. Seasonal variation in leaf mass and N content per leaf area (LMA, (**a**,**b**); N_{area}, (**c**,**d**)) associated with *A. ordosica* (AO, left-side panels) and *S. psammophila* (SP, right-side panels), respectively. Error bars represent standard error. Asterisks represent significant differences for individual measurements during the same DOY during both wet and dry summer periods ($p < 0.05$).

The seasonal patterns in N_{area} were generally similar to those of the LMA, while in the wet summer, N_{area} reached the maximum at the end of summer, and the peak dates were about 60 days behind the LMA. Compared with the wet summer, the dry-summer mean N_{area} for *A. ordosica* and *S. psammophila* decreased by 17.9 and 17.7%, respectively. Regardless of wetness, the mean N_{area} associated with *A. ordosica* was largely greater than the corresponding value in *S. psammophila* (Figure 4; Table 2).

3.4. Seasonal Changes in the PNUE and IWUE and Their Controlling Factors

The seasonal PNUE during the wet summer was generally lowest in early summer, peaking in August (Figure 5c,d). The mean PNUE of *A. ordosica* was about twice that of *S.*

psammophila. During the dry summer, seasonal variations in the PNUE were mostly similar to the variation observed in both A_{sat} and g_s (Figure 3a–d). The mean PNUE in *A. ordosica* and *S. psammophila* significantly decreased from the wet to the dry summer, with reductions of 35.7 and 47.4%, respectively.
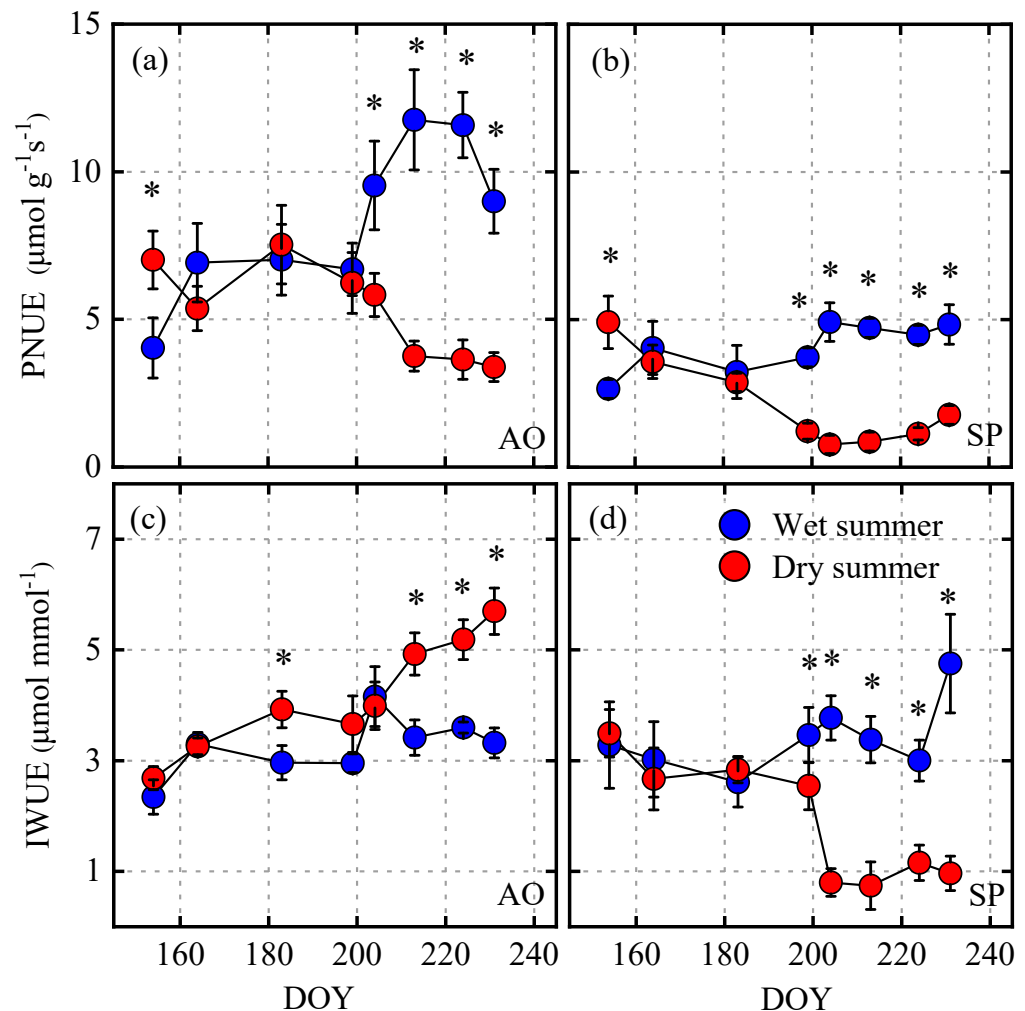

Figure 5. Seasonal variation in photosynthetic N and instantaneous water use efficiencies (PNUE, (**a**,**b**); IWUE, (**c**,**d**)) in *A. ordosica* (AO, left-side panels) and *S. psammophila* (SP, right-side panels) for the wet and dry summer periods, respectively. Error bars represent standard error. Asterisks represent significant differences for individual measurements during the same DOY during both wet and dry summer periods ($p < 0.05$).

Unlike the seasonal trends in the PNUE during the wet summer, the seasonal IWUE usually fluctuated around 3 µmol mmol^{-1} during the wet summer, irrespective of species. The response of the IWUE to long-term drought varied as a function of species (Figure 5c,d). The instantaneous water use efficiency in *A. ordosica* continuously increased as the drought persisted, eventually reaching a net increase of about 28% during the wet summer. In *S. psammophila*, the IWUE steadily decreased during the dry summer and was usually <1.2 µmol mmol^{-1} at the end of the July–August period. There was a significant interaction effect between season and species on the IWUE (Table 2).

The results revealed that the seasonal variations in the plant RUEs during the wet summer were largely linked to variations in g_s (Figure 6). Both the PNUE and IWUE increased with increasing g_s (Figure 6c–f). During the dry summer, the PNUE in *A. ordosica* generally decreased with decreasing g_s, VWC, and N_{area} (Figure S2; Table S1), whereas in *S. psammophila*, the PNUE decreased with increasing T_a and decreasing g_s, VWC, LMA,

and N_{area} (Figure S2; Table S1). The seasonal IWUE in *A. ordosica* during the dry summer increased with decreasing g_s, LMA, N_{area}, and VWC (Figure S3; Table S1). In contrast, the IWUE in *S. psammophila* decreased with decreasing g_s and VWC and increasing T_a (Figure S3; Table S1).
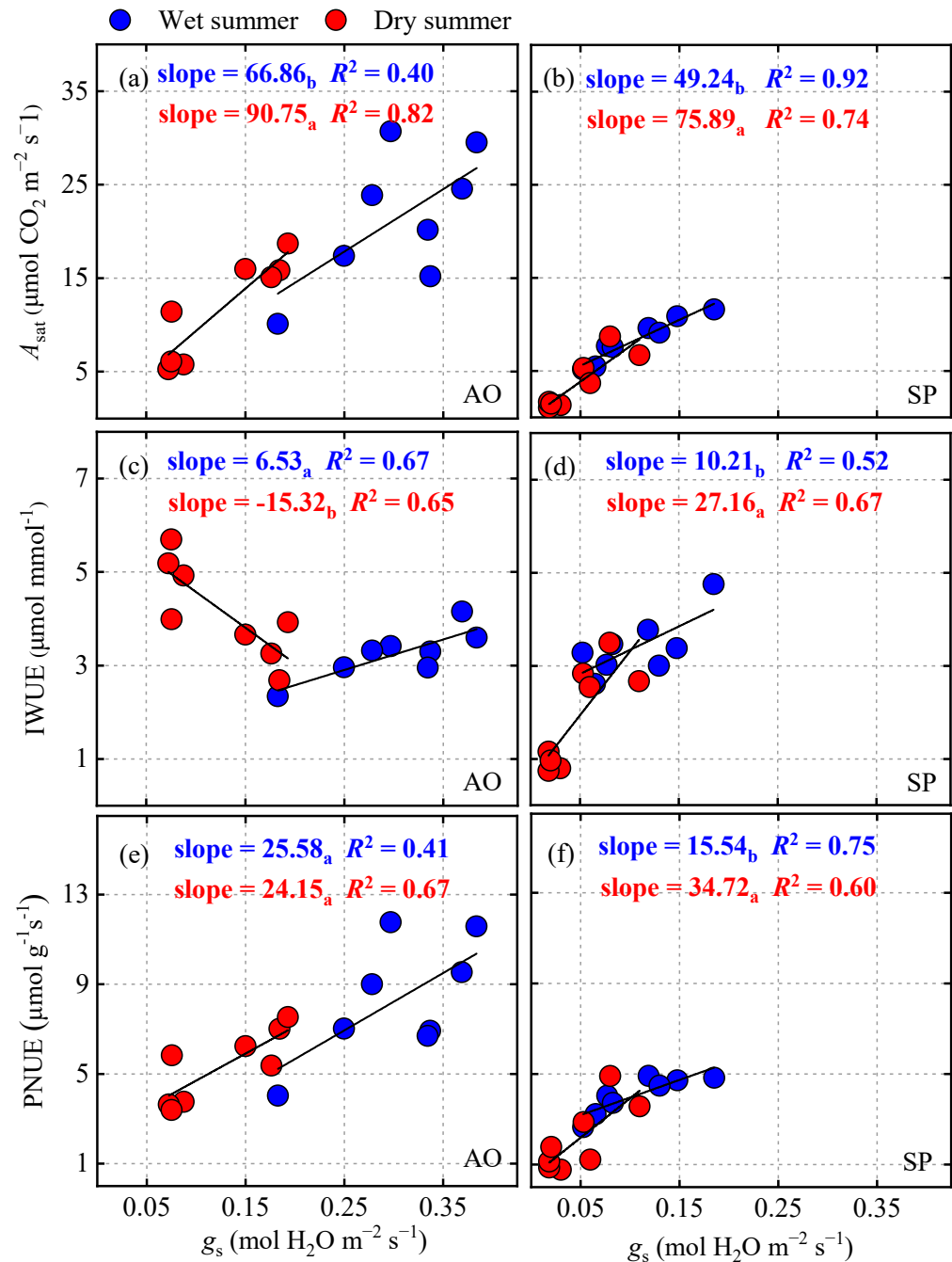

Figure 6. Pairwise relationships between light-saturated net C assimilation rates (A_{sat}, (**a**,**b**)), instantaneous water use efficiency (IWUE, (**c**,**d**)), photosynthetic N use efficiency (PNUE, (**e**,**f**)), and stomatal conductance (g_s) associated with *A. ordosica* (AO, left-side panels) and *S. psammophila* (SP, right-side panels), respectively. Subscripted letters that differ, both across and within panels, denote statistically significant differences (i.e., $p < 0.05$).

4. Discussion

4.1. Seasonal Response of Leaf Photosynthesis to Long-Term Summer Drought

Compared with the wet summer, the severe summer drought significantly reduced A_{sat} in *A. ordosica* and *S. psammophila* by 45.1 and 55.4%, respectively. These results were consistent with reductions observed in C assimilation in deciduous plants exposed to drought [33,49]. These results support the conclusion that *A. ordosica* had a greater tolerance to drought than *S. psammophila* (Table 2; [12,38,42]).

It is well documented that under drought, plants optimize C assimilation while minimizing water losses by reducing g_s [50,51]. The strong coupling between net assimilation and g_s reveals the importance of water in controlling assimilation rates [8,42,52]. Some studies have shown that there is a diversity of stomatal responses among plant species [49,53]. Compared to the wet season, the C assimilation rate in two xerophytic shrubs, namely *Ipomoea carnea* and *Jatropha gossypifolia*, decreased during dry seasons, while the relative stomatal limitation (L_s) in *J. gossypifolia* decreased by 27% [54]. Down-regulation of photosynthesis in some Mediterranean shrubs (e.g., *Erica multiflora* and *Eugenia uniflora*) was strongly coupled with metabolic damage and biochemical restrictions and depended less on g_s [9,55].

In this study, A_{sat} tended to decrease as g_s decreased in both the wet and dry summers (Figure 6a,b). The slopes of the A_{sat}-to-g_s relationships for each species were clearly steeper during the drought, indicating that drought stress increased the sensitivity of g_s in both shrubs. This is consistent with findings associated with plants in savanna communities [8,56]. Moreover, although the degree of the decrease in g_s of the two species in the dry summer was very close, the mean g_s of *S. psammophila* in the dry summer was only about 38% of that of *A. ordosica*. This result indicated that *S. psammophila*, with a low carbon assimilation rate, underwent stricter stomatal closure during the dry summer.

Drought adjustments of biochemical and structural traits indicated the changes in activity of the photosynthetic apparatus [31]. In our study, the differences in the LMA between species were greater than the seasonal differences (Table 2). This was consistent with prior results [21]. Some studies have reported that tropical trees and blue oak trees can maintain a stable leaf N content even after being exposed to severe drought [8,57,58]. At our study site, we observed a rapid decrease in N_{area} during the dry summer in both species. This result was consistent with previous studies concerning xerophytic shrubs [43,59]. Moreover, the down-regulations of the quantum yield of photosystem II (PSII) and leaf photosynthetic capacity induced by drought were generally related to the decrease in the leaf nitrogen content [60]. The high N losses and low A_{sat} values in *S. psammophila* during drought, compared to *A. ordosica*, suggested that *S. psammophila* may have suffered more from extensive metabolic damage than *A. ordosica* [42,50].

4.2. Tradeoffs between the IWUE and PNUE during Long-Term Summer Drought

The means of the IWUE for the two xerophyte shrubs were well within the range (i.e., 1.0–6.5 µmol mmol^{-1}) reported for 14 separate shrubland species [39,61–63]. We found that the two xerophytic species took diverse water use strategies in the wet summer. Despite the fact that there were no species differences in the IWUE during the wet summer between *A. ordosica* and *S. psammophila*, the transpiration rate in *A. ordosica* during the wet summer was significantly greater than the rate in *S. psammophila* (Figure 3e), indicating that *A. ordosica* used a more wasteful water use strategy during the wet summer period than *S. psammophila* [42]. A similar water-wasting strategy was observed in a desert annual sunflower, *Helianthus anomalus*, whereby more leaf N was transported by transpiration flow [64]. This could explain why the leaf N content and PNUE in *A. ordosica* were substantially higher than the corresponding values in *S. psammophila*. We infer that under conditions of high soil water availability, xerophytic species that invest more N resources into photosynthesis are capable of assimilating more C.

Temporal variations in RUEs are affected by climatic factors [6,10], plant physiology [12,65], and soil nutrient content [15]. Understanding the dynamics in the IWUE and

PNUE and their underlying regulatory mechanisms can improve our ability to predict the effects of climate change on C and water cycles in dryland ecosystems. We found that for the two shrub species, whether in the wet or dry summer conditions, the seasonal variations in the IWUE and PNUE were largely dependent on changes in g_s, which is consistent with prior studies that have reported strong correlations between plant resource acquisition and g_s [12]. Both the IWUE and PNUE were shown to respond differently to the wet and dry summer conditions. This suggests that xerophytic shrubs have elevated physiological plasticity in terms of resource acquisition. The seasonal adjustments in the water and N use strategies in the xerophytic shrubs during the severe summer drought were largely triggered in response to reductions in soil moisture, a result that is comparable to studies on *Cneorum tricoccon* [66], *Ephedra alata* [67], and *Stipa breviflora* communities [68]. The drought-induced reduction in the PNUE in the two species was consistent with previous studies [57]. Some studies have reported that the reduction in PNUE under drought stress was completely caused by assimilation loss [8,31]. In our study, the drought adaptation of the PNUE was closely related to stomatal closure and leaf nitrogen loss (Table S1). The decrease in the PNUE was mainly due to the greater drought sensitivity of the net assimilation rate compared to N_{area}, and this was consistent with findings in other drought-tolerant species [21].

The relationship between dissimilar RUEs may exhibit various patterns at different spatiotemporal scales and environmental settings [23,35]. We found that the seasonal relationship between the IWUE and PNUE during the dry summer depended on the response of the IWUE to long-term drought at the species level. The tradeoff by sacrificing the PNUE while increasing the IWUE was only observed in highly drought-tolerant species such as *A. ordosica* (Figure 7). This result contradicts the belief that patterns of the IWUE and PNUE in co-existing plant species tend to converge [28,29].
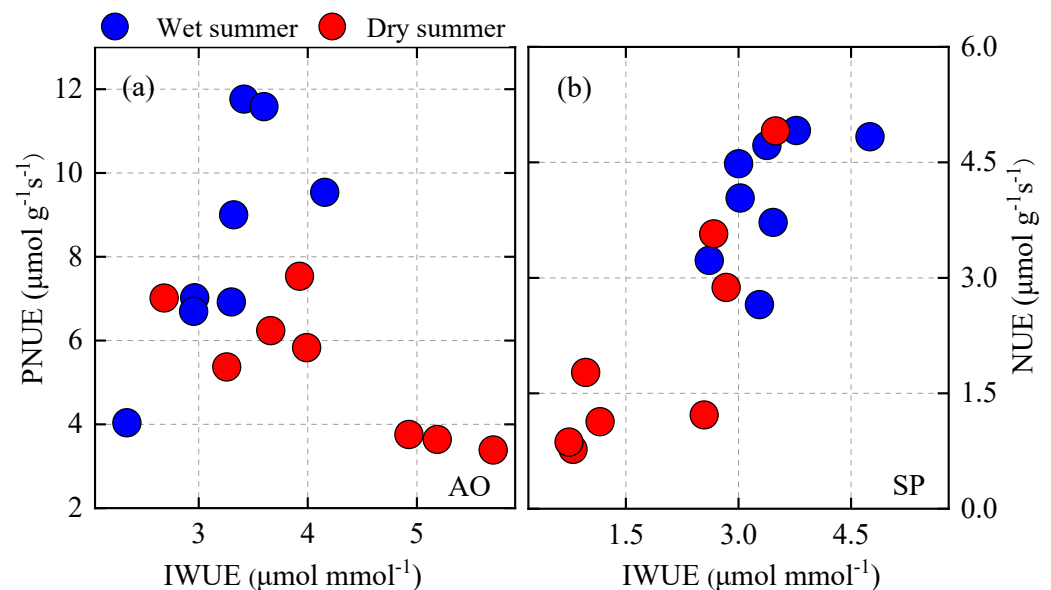

Figure 7. Seasonal relationships between instantaneous water and photosynthetic N use efficiencies (i.e., IWUE and PNUE) in *A. ordosica* (AO, (**a**)) and *S. psammophila* (SP, (**b**)) during the wet and dry summer periods.

In water-limited environments, photosynthetic C gains and water losses by transpiration are in a permanent state of adjustment, as both are regulated in opposite directions with changes in g_s [28]. However, the duration of drought played a critical role in regulating the response of the IWUE [9,10]. During the short-term drought, the observed increase in the IWUE was largely due to the fact that the sensitivity of the net assimilation rate to g_s was often lower than the sensitivity of the transpiration rate to g_s [15,69]. During a long-term drought, a slow or conservative strategy may become disadvantageous because

slow traits are costly to maintain [3]. A sustained low g_s may amplify the limitations of stomatal closure on plant physiology. For example, a further decrease in g_s causes corresponding decreases in F_v/F_m and the rubisco initial activity [70], further affecting the IWUE [33,34]. Some studies have emphasized interspecific differences in plasticity in the IWUE [51,71], with the difference largely determined by differences in the regulation of stomatal conductance and transpiration [70,72]. We found significant species differences in the ability to regulate the IWUE via g_s, as suggested by the range in g_s and the degree that the stomata could remain open during the dry summer conditions (Figure 3; Figure 8). In general, *A. ordosica* presented a higher plasticity to drought by maximizing A_{sat} during favorable conditions in early summer and regulating g_s (causing the IWUE to increase) during prolonged drought. However, the low sensitivity of E to changes in g_s in *S. psammophila* suggested an even weaker control of E under extremely low g_s (Figure 8). Our research illustrated the need to assess plasticity in g_s when addressing plant adaptation to long-term summer drought.
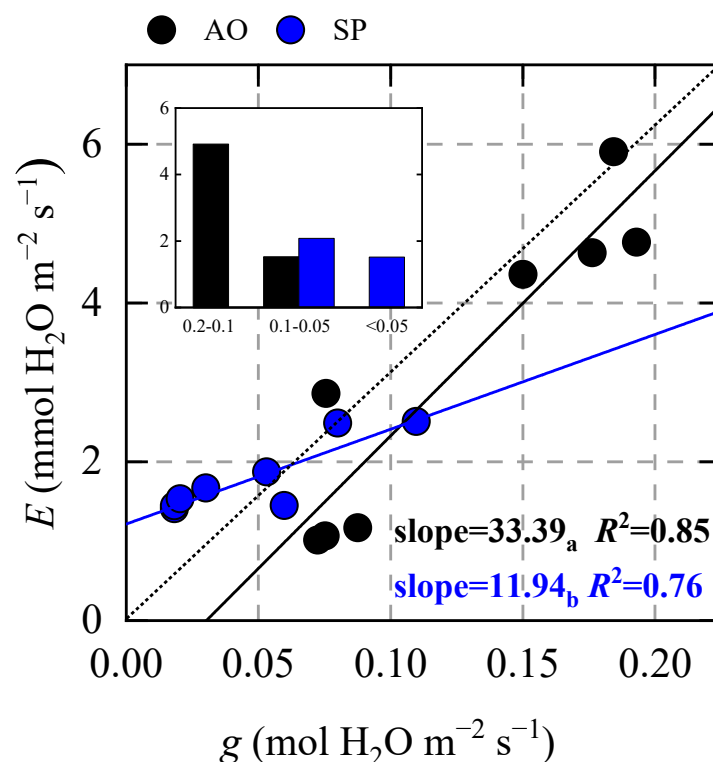
Figure 8. Relationships between transpiration rate (E) and stomatal conductance (g_s) in *A. ordosica* (AO) and *S. psammophila* (SP) during summer drought. The inset illustrates changes in transpiration rate (E) under various levels of stomatal conductance (g_s) in the two shrub species. The different subscripted letters assigned to slopes denote statistically significant differences (i.e., $p < 0.05$).

5. Conclusions

Whether during wet conditions or drought, the gas exchange parameters and PNUE in *A. ordosica* were greater than those in *S. psammophila*. *A. ordosica* maintained greater photosynthetic performance and an increased IWUE during severe summer drought, supporting the belief that *A. ordosica* is more tolerant of drought than *S. psammophila*. The seasonal trends in the IWUE and PNUE were more highly dependent on changes in stomatal conductance. The seasonal adjustments in both the IWUE and PNUE in the xerophytic shrubs during drought responded to local reductions in soil moisture. Moreover, the seasonal relationships between the IWUE and PNUE depended more on the response of the IWUE at the species level, largely because of differences in the plasticity of stomatal conductance. Our findings emphasized that physiologically plastic species can maintain

their positions in extreme hot–dry environments by constantly adjusting their rate of photosynthesis and resource use efficiency.

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