

Ting Zou · Yan Li · Hao Xu · Gui-Qing Xu

## Responses to precipitation treatment for *Haloxylon ammodendron* growing on contrasting textured soils

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**Abstract** The responses to precipitation of *Haloxylon ammodendron* (C.A. Mey.) Bunge (Chenopodiaceae), a small xerophilous tree growing on contrasting textured soils, were evaluated under no, natural, and double precipitation treatments during the entire growing season of 2006. The contrasting textured soils are sandy and heavy textured, and both are the original habitat of *H. ammodendron* at the south edge of Gubantonggute Desert, Central Asia. Photosynthesis, leaf water potential, transpiration, water use efficiency and leaf biomass production were monitored throughout the growing season. Root distribution of *H. ammodendron* was evaluated at the end of the experiment. Overall, this small tree did not show significant response to a large summer precipitation pulse or precipitation treatments, in terms of photosynthetic carbon assimilation on either soil. The leaf water potential, transpiration, and water use efficiency appeared to be highly sensitive to a large precipitation pulse and precipitation treatments in sandy soil; and leaf biomass production was also much higher for plants in sandy than that of heavy-textured soil. In sandy soil, defoliation occurred when pre-dawn leaf water potential dropped below  $-3.0$  MPa, while in heavy-textured soil, defoliation occurred when pre-dawn leaf water potential dropped below  $-3.75$  MPa. For similar above-ground parts, the small trees at the sandy site developed much deeper root systems and had nearly double the surface area of feeder roots compared to those at the heavy-textured site. Partially owing to the deeper and larger root system, *H. ammodendron* growing at coarse-textured site was in better water conditions

than those at heavy-textured site under the same climatic conditions.

**Keywords** Biomass allocation · Branch growth · Leaf water potential · Photosynthesis · Root distribution

### Introduction

Water is a key factor limiting ecosystem processes (e.g., carbon fixation, plant growth, and respiration) and functional responses (e.g., net primary production or NPP) (Cheng et al. 2006; Dube and Pickup 2001; Ehleringer et al. 1999; Sala et al. 1997) in arid and semiarid regions, where pulses of precipitation are the primary water source (Cheng et al. 2006). Precipitation patterns (event size, timing, and frequency) and distribution further interact with local topography and soil texture, strongly mediating the dynamics of plant water uptake through their control on plant water availability (Hamerlynck et al. 2004; Huxman et al. 2004; McAuliffe 1994; Noy-Meir 1973). Small-scale variation in vegetation, soil surface cover, and soil texture, alters the amount of water available to plants (Whitford 2003). Different plant species and functional groups differ in their response to precipitation pulses (Cheng et al. 2006; Donovan and Ehleringer 1994; Dougherty et al. 1996; Flanagan et al. 1992; Golluscio et al. 1998; Loik 2007; Phillips and Ehleringer 1995). Large precipitation pulses that percolate deep into the soil profile may provide a water source that can be utilized by shrubs, which are typically not as sensitive to summer precipitation as herbaceous species (Schwinning et al. 2003). However, to what extent these large summer pulses of water are utilized by woody species will ultimately depend on the combination of soil hydraulic characteristics and plant water use strategy (Fravolini et al. 2003; Hacke et al. 2000; Hultine et al. 2006; Schlesinger and Pilmanis 1998; Sperry and Hacke 2002). There should be more plant-available water in sandy soils than in finer-textured clay soils due to the high infiltration rate, deep percolation,

T. Zou · Y. Li (✉) · H. Xu · G.-Q. Xu  
Fukang Station of Desert Ecology and Key Laboratory of Oasis Ecology and Desert Environment, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, 40-3 South Beijing Road, 830011 Urumqi, Xinjiang, People's Republic of China  
E-mail: liyan@ms.xjb.ac.cn

T. Zou  
Graduate School, Chinese Academy of Sciences, 19A,  
Yu-Quan Road, 100049 Beijing, People's Republic of China

and less evaporation of capillary water in coarse soils (Hamerlynck et al. 2002; McAuligge 1994). Although clay soils hold more water than sandy soils, water is more tightly bound to the fine clay particles than to larger sand particles (Nilsen and Orcutt 1996), so consequently the rates of infiltration are lower and surface evaporation is higher than for coarse soils. Previous researches showed that under similar climatic conditions, vegetation in arid habitats is substantially more vigorous and abundant on coarse, sandy soils than fine-textured soils (Fravolini et al. 2005; Noy-Meir 1973). This inverse texture effect is likely a result of differences in evaporation with soil texture rather than differences in drainage (Noy-Meir 1973). Soil texture determines soil hydraulic characteristics, which can have severe consequences for survival of desert plants. Explorations of physiological response and water use by the same species to the same precipitation treatment in contrasting soil textures, and the differences in utilizing precipitation at one site during the growing period, are necessary in understanding the mechanisms of desert plant adaption to seasonal and geographical changes in soil moisture availability and how these influence both the physiological and morphological features of desert plants.

*Haloxylon ammodendron* (C.A. Mey.) Bunge (Chenopodiaceae), a sub-tree xerophilous C4 plant dominates many areas of Asian deserts (60°N–111°N and 36°E–48°E) with average annual rainfall between 30 and 200 mm. In China, *H. ammodendron*, as an important component of old Mediterranean flora widely spread in the Zhunger Basin, northeast of the Tarim Basin and several other desert areas on a range of soils (Wu 1980). This species is of great ecological and economic importance, not only because it can survive harsh environmental conditions but it can also stop wind erosion of sand. *H. ammodendron* has many xeromorphic characteristics (Fahn and Cutler 1992; Huang et al. 2003) of adapting to drought, salinity, poor nutrition, strong wind, sand movement, and high light intensity. For example, the leaves are reduced and the succulent branches perform the function of carbon assimilation (Huang et al. 1997).

Soil water availability is critical to plant growth and can vary among and within sites (Larcher 2003; Sultan et al. 1998). Desert plants are generally well adjusted to its fluctuations through a variety of physiological, morphological adaptations, and life-history strategies (Chesson et al. 2004), as they are typically exposed to extreme conditions driven chiefly by occasional pulses of precipitation and high atmospheric evaporative demand. However, there is a paucity of field studies on response to precipitation changes for *H. ammodendron* growing at sites of contrasting soil textures, and at both physiological and morphological levels. Therefore, considering the anticipated changes in precipitation in this region (Kripalani et al. 2007), we conducted a field experiment on *H. ammodendron* growing at sandy and heavy-textured soil sites with precipitation manipulated by rain-shelter and artificial rainfall. Through applying

precipitation treatments on *H. ammodendron* growing in contrasting soil textures and observing the responses at physiological and morphological levels, we expected to achieve two objectives. The first was to explore experimentally the similarity and differences in responses of *H. ammodendron* at two sites to large precipitation pulse. The second objective was to investigate how *H. ammodendron* achieved the respective optimal physiological condition and growth at the contrasting soil sites through effective morphological adjustment at individual scale.

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## Materials and methods

### Study sites and precipitation

Experiments were conducted during the entire growing season of *H. ammodendron* in 2006 (Julian Days 144–252) in its native habitat adjacent to the Fukang Station of Desert Ecology, Chinese Academy of Sciences, in the hinterland of the Eurasian continent (44°17'N, 87°56'E, 475 m a.s.l.). This species naturally occurs in very different soil textures: sandy soil at the south edge of Gurbantonggut Desert (44°15'N–46°50'N, 84°50'E–91°20'E), and heavy-textured soil at the fringe of the alluvial plain (hereafter referred to as “sandy” and “heavy-textured” soils, respectively). The two sites were approximately 8 km apart without geomorphic change.

This region has a continental arid temperate climate, with a hot dry summer and cold winter; annual mean temperature is 6.6°C, annual mean precipitation is ≈160 mm, which is about evenly distributed throughout the year; annual pan evaporation is about 1000 mm. During the experiment, the precipitation at both sites was recorded by rain gauges, and it proved that difference in precipitation between the two habitats was negligible (40.7 mm at sandy site and 40.8 mm at heavy-textured site during the whole growing season). Other meteorological data, such as air temperature, humidity, global radiation, wind speed and direction etc., were obtained by an automatic weather station (Campbell Scientific, Logan, Utah, USA) installed between the two sites.

### Precipitation manipulation and plant material

Three precipitation treatments were applied in each habitat. No precipitation treatment was realized by a 40 × 40 m removal awning (rain-shelter) installed on a two rail-track, which was moved onto the plot when it was raining and moved away when the rain was over. Natural precipitation is just a marked plot of 40 × 40 m with no treatment carried out on the *H. ammodendron* inside. Double precipitation was realized by adding an equal amount of irrigation after each rainfall over a 40 × 40 m plot. Irrigation was carried out from a portable sprinkler system at the height of 3.5 m, about 1 m

above the plant canopy. Irrigation speed was controlled to prevent runoff and surface runoff has not been observed at the two sites during precipitation and irrigation.

*H. ammodendron* is a sub-tree xerophilous plant that is native to a variety of central Asian and African desert habitats, including gravel desert, heavy-textured desert soil, and sandy desert. Within very short distances with the same climate, the habitats of *H. ammodendron* may change from sand soil to heavy-textured, which is ideal for the aforementioned study. *H. ammodendron* is a major dominant species at both experimental sites. In each treatment, five plants of approximately average age and size were selected around the center of the plot for physiological monitoring and biomass observation. The selected plants were on average 1.70 m in height and 1.05 m in canopy radius and at about the same age (25–30 years old).

#### Soil characterization and analyses

Five samples per soil layer (0–20, 20–40, and 40–150 cm deep) were taken from both sites and analyzed with a laser diffraction system (Sympatec GmbH, System-Partikel-Technik, and Clausthal-Zellerfeld, Germany) to determine soil texture composition. The respective percentages of sand, silt, and clay of the sandy soil were 85, 13.7, and 1.3%, and for heavy-textured soil were 22.7, 68.9, and 8.4%.

Changes in soil moisture content (SMC) were monitored gravimetrically at both sites. Soil samples were taken randomly by auger over 0–2 m depth at 0.1-m intervals, and repeated three times at each precipitation treatment at both sites. SMC was determined by a conventional oven-drying and weighing method.

#### Measurement of leaf water potential ( $\Psi_L$ ), transpiration, and photosynthesis

We measured pre-dawn ( $\Psi_{pd}$ ) and midday leaf water potentials ( $\Psi_m$ ) on the three precipitation treatments and at the two sites using a model 3005 Pressure Chamber (PMS Instrument Company, Albany, OR, USA). All measurements were on clear days throughout the growing season.  $\Psi_{pd}$  was measured 20 min before sunrise, and  $\Psi_m$  around solar noon. Small branches with sufficient leaves were selected, and the sampling was repeated twice per plant. Thus, for each treatment, five replicates were taken to determine the average value of  $\Psi_L$  at a given time.

The transpiration rate ( $T_r$ ) was taken as the sap flow rate measured by a compensated heat-pulse system, considering that there is strong co-ordination between liquid phase (sap flow) and vapor phase (transpiration) water transport in plants (Meinzer 2002). The heat pulse system was developed original by Cohen et al. (1988) for

small stems or branches with its linear sensor measuring average sap velocity in the stem/branch (Cohen and Li 1996). Thirty tiny heat-pulse probes (five per treatment at each site) were installed on branches with diameters of 8–15 mm, and  $T_r$  for each branch recorded every 0.5 h. To minimize the effect of wounding wood matrix, probes were allowed to stay in one position not longer than 2 weeks before it was moved to another position. To overcome the effect of variation in branch size, the  $T_r$  value was normalized on a leaf-area basis. To quantify leaf area of each branch, all foliage on each selected branch was photographed every 2 weeks with a  $6 \times 10^8$  pixel digital camera (Canon 300D, Canon Inc., Tokyo, Japan). The leaf surface area of each branch was calculated from the photographs using CI-400 CIAS software (Computer Imaging Analysis Software, CID Co., Logan, UT, USA). The  $T_r$  value was then converted to a leaf-specific value according to the leaf surface area of each branch.

The photosynthetic light–response curves of the species were measured by a Li-6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA). In-chamber photosynthetic photon flux density (PPFDi) was controlled by  $20 \times 30$  mm leaf chamber with a light source (red + blue 6400-02B). The PPFDi gradient range was 0–2200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , at intervals of 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The gas flow rate was set at 400  $\mu\text{mol s}^{-1}$  to maintain a reference relative humidity of 20–30%, which is close to ambient humidity. This resulted in leaf-to-air vapor pressure deficits ( $\text{VPD}_{\text{leaf}}$ ) of 2–3 kPa. Chamber temperature was controlled at 30°C. A  $\text{CO}_2$ -injecting device was attached to the system to control reference  $\text{CO}_2$  concentration at 400  $\mu\text{mol mol}^{-1}$ . The measurements were taken at 1000–1500 h, local time. For plants in each precipitation treatment, two sets of leaves were measured from each of the five sample plants. The measured leaves were those that were youngest, mature, and healthy. The detailed procedure was described by Xu and Li (2006). Advanced regression analysis of the non-linear curve showed that the relationship between net photosynthetic rate ( $P_n$ ) and PPFDi was best fitted by exponential MnMolecular function  $y = A [1 - e^{-k(x-x_c)}]$ , in which  $x$  is PPFDi,  $y$  is net photosynthetic rate, parameter  $A$  is net photosynthetic rate at light saturation point ( $P_s$ ),  $x_c$  is PPFDi at the light compensation point ( $I_c$ ) and  $k \cdot A$  is apparent quantum efficiency of photosynthesis ( $\Phi$ ). From a light–response curve fitted to the average data from each set of reduplicate photosynthesis experiments, the values of  $P_s$ ,  $I_c$ , and  $\Phi$  were calculated to indicate the photosynthetic capacity in each condition. The notation and definition of each parameter follows that of Sage (1994). The photosynthetic water-use efficiency [ $\text{WUE} (\mu\text{mol CO}_2 \cdot \text{mmol}^{-1} \text{H}_2\text{O})$ ,  $P_n (\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1})/T_r (\text{mmol m}^{-2} \text{ s}^{-1})$ ] was calculated from  $P_n$  and  $T_r$  (obtained from sap flow measurement) at  $\text{PPFD} = 1600 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ .

The data “before precipitation” and “after precipitation” were collected at two sites on two continuous days before or after the precipitation day.

## Measurement of leaf area and branch biomass

Above-ground biomass accumulation was observed throughout the growing season. Under each treatment, ten well-growing branches were selected and labeled on each of the five sample plants. All the foliage on each branch was photographed with a  $6 \times 10^8$  pixel digital camera (Canon 300D, Canon Inc, Tokyo, Japan), at intervals of 2 weeks during the whole growing season. The total leaf surface area of each branch was calculated from the photographs using CI-400 CIAS software (Computer Imaging Analysis Software, CID Co., Logan, UT, USA). Change in the stem surface area of the labeled branch was traced in the same way. At the end of the experiment (31st August, Julian Day 243), the labeled branches were cut. Fresh and dry mass of leaves and twigs on each branch were weighed to define the relationship between surface area and dry mass of the foliage/branch of each plant. On the basis of this relationship, the surface area of each branch was converted into its dry mass. To eliminate the effect of initial size difference among branches, a weighing average was employed for each measurement. The weighing factor was taken as the reciprocal of the ratio between initial dry mass of a branch and the initial average dry mass of all measured branches at one site. This way, each branch was equally represented in the average. After taking this weighed average, branch growth rate during the period between every two sequential measurements was calculated to represent the general condition of foliage area expansion and branch biomass accumulation under each precipitation treatment.

## Root morphological investigation

The investigation of root-system distribution was done at the end of the experiment (early September, Julian Days 248–252). With the intention of minimizing destruction, only three plants in the natural precipitation treatment at the two sites were excavated to investigate the morphological characteristics and water-use strategies of the intact root systems. The inner diameter of the root excavation ditch was 12 m. For each plant, the surface area of fresh feeder roots was recorded and calculated for each 0.1 m of the depth in the profile, and used to derive an overview of the vertical root distribution. For the detailed procedure, see Xu and Li (2006).

## Data analysis

All statistical tests were performed with SPSS (Ver. 16.0) for Windows. Descriptive statistics were used to calculate means and standard errors for each set of replicates. A two-way ANOVA with precipitation treatment  $\times$  soil type was performed to test the effect of precipitation treatments, soil textures, and their interactions, SMC,  $\Psi_{pd}$ ,  $\Psi_m$ ,  $T_r$ ,  $P_s$ ,  $I_c$ ,  $\Phi$ , WUE, leaf area per branch, branch growth rate as response variable. One-way ANOVA, followed by Tukey's or Tamhane's multiple comparison tests were used to test differences in measured means of variable for different treatments at the same site.

## Results

### Soil moisture content before and after large precipitation pulse

For 37 days before the large precipitation pulse on 7 July 2006 (Julian Day 188, 22.8 mm), no significant precipitation pulses occurred (Table 1). After the large precipitation pulse on Julian Day 188 in July (Table 1), SMC in the 0–0.3 m layer was significantly influenced in the sandy soil ( $F = 7.70$ ,  $P = 0.022$ ) (Fig. 1a), while the SMC in the 0–0.1 m layer was significantly influenced in the heavy-textured soil ( $F = 27.69$ ,  $P = 0.001$ ) (Fig. 1b). SMC of the deep layers remained stable at both sites (Fig. 1). Other rainfall events in the growing season were not large enough to have a significant effect on the soil moisture content (Table 1).

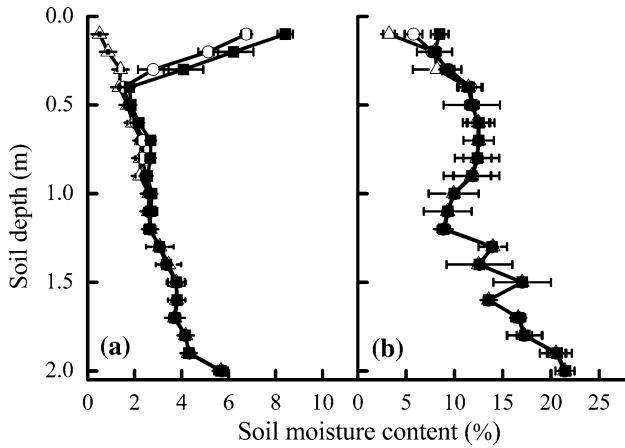
### Physiological responses after large precipitation pulse

As shown in Fig. 2,  $\Psi_{pd}$  significantly responded to changes in SMC over the 10-day observation period ( $F = 4.92$ ,  $P = 0.014$ ). At both sites, precipitation treatment affected  $\Psi_{pd}$  and  $\Psi_m$  significantly ( $P < 0.001$ ), and the change for  $\Psi_{pd}$  and  $\Psi_m$  under natural and double precipitation treatments significantly differed from no precipitation treatments ( $P = 0.05$ ) (Fig. 2). The decline in  $\Psi_L$  after the rain pulse showed a similar pattern among treatments and across sites, but the relative differences were maintained. Prior to the large precipitation pulse,  $\Psi_{pd}$  was higher at the sandy than the heavy-textured site. Following the precipitation,  $\Psi_{pd}$  and  $\Psi_m$  showed a greater increase at the sandy

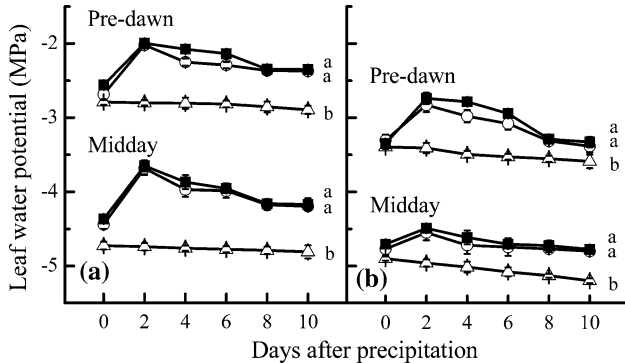
**Table 1** Precipitation pulses during the growing season of 2006 at two sites

Precipitation (mm)	June (Julian Day)				July (Julian Day)				August (Julian Day)			
	155	166	167	170	185	188	201	205	217	229	241	243
Sandy site	1.7	2.6	0.4	1.3	0.4	22.8	3.8	1.2	0.9	3.9	0.8	0.9
Heavy-textured site	1.6	2.8	0.6	1.4	0.3	22.8	3.5	0.8	1.0	4.0	1.0	1.0





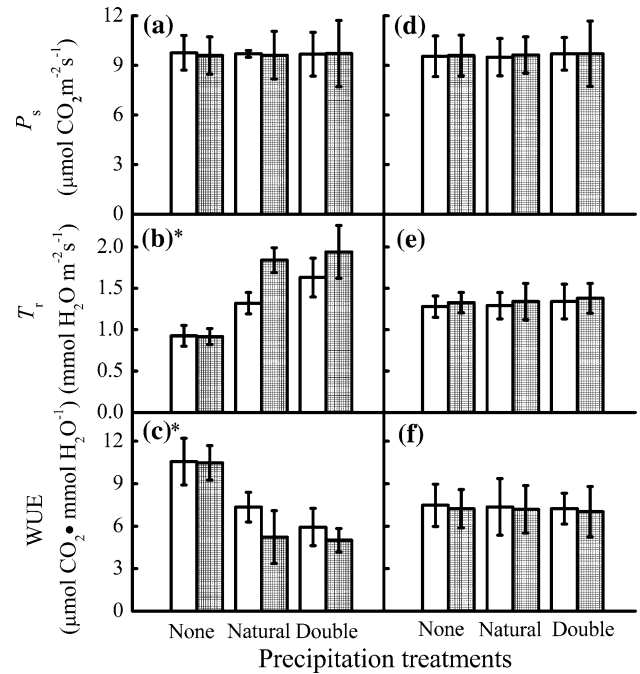
**Fig. 1** Soil moisture content (%) under no precipitation (*triangle with line*), natural precipitation (*circle with line*) and double precipitation treatment (*square with line*) at two contrasting textured soils (**a, b**) right after a large precipitation pulse on Julian Day 188 (22.8 mm). Each value is the mean for three replications  $\pm$  SE. Error bars represent the standard error of the mean



**Fig. 2** Daily changes of leaf water potential for *H. ammodendron* following a large precipitation (22.8 mm) under no precipitation (*triangle with line*), natural precipitation (*circle with line*) and double precipitation treatment (*square with line*) across two contrasting soil textures with two-way ANOVA ( $P = 0.05$ ) (**a, b**). Day 0 is 6 July 2006 (Julian Day 188). Each value is the mean for five replications  $\pm$  SE. Error bars represent the standard error of the mean. Different lowercase letters indicate significant differences under three precipitation treatments on each day with one-way ANOVA ( $P = 0.05$ )

than the heavy-textured site, although the differences were not statistically significant. Overall, *H. ammodendron* at the sandy site maintained less negative  $\Psi_{pd}$  and  $\Psi_m$  than at the heavy site. Moreover, the rate of  $\Psi_{pd}$  and  $\Psi_m$  decreases after the precipitation was bit slower at the sandy than at the heavy-textured site (Fig. 2).

The photosynthetic capacities of *H. ammodendron* after the large precipitation pulse did not significantly differ among treatments and between sites ( $P = 0.05$ ) (Fig. 3a–f). However, at the sandy site,  $T_r$  was significantly different among treatments ( $F = 7.30$ ,  $P = 0.025$ ) (Fig. 3b), with the lowest at the no-rainfall treatment. Consequently, the photosynthetic WUE ( $F = 17.10$ ,  $P = 0.003$ ) (Fig. 3c) was highest for the

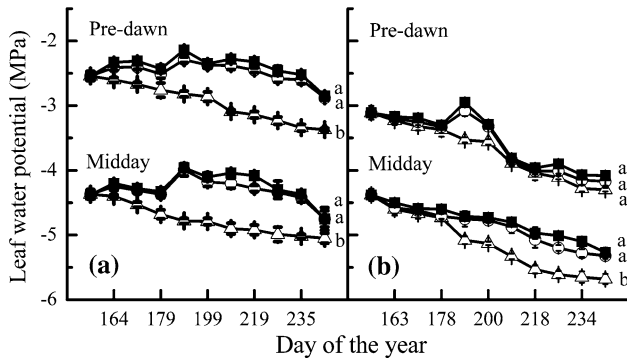


**Fig. 3** Comparison of physiological response in drought (*open rectangle*) and after a large precipitation (22.8 mm) (*filled rectangle*) among three precipitation treatments in sandy soil (**a–c**) and heavy-textured soil (**d–f**) for *H. ammodendron* with two-way ANOVA ( $P = 0.05$ ). Each value is the mean for five replications  $\pm$  SE. Error bars represent the standard error of the mean. The asterisk indicates significant difference under three precipitation treatments with one-way ANOVA ( $P = 0.05$ )

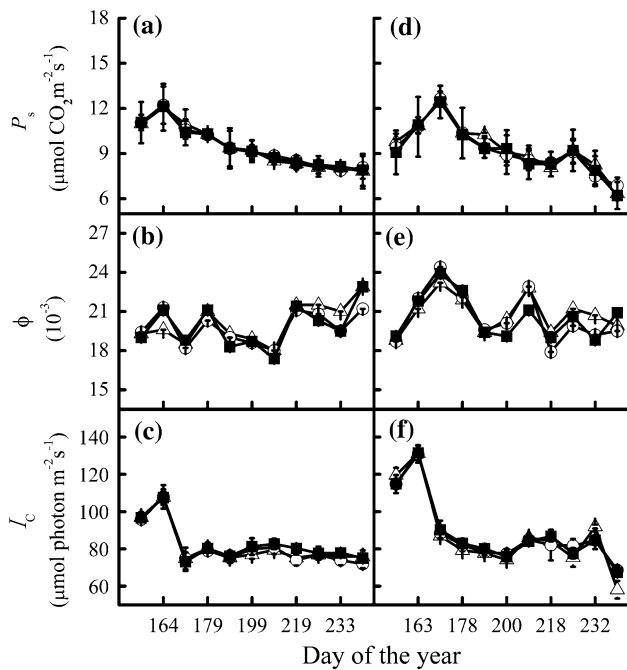
no-rainfall treatment. At the heavy-textured site,  $T_r$  and photosynthetic WUE were not significantly different among treatments (Fig. 3e, f).

### Seasonal variations in plant physiology

At both sites, plants that received the double precipitation had significantly higher  $\Psi_m$  than those under no-precipitation treatment, but not significantly higher than plants in the natural precipitation treatment during the growing season ( $F = 12.88$ ,  $P < 0.001$ ) (Fig. 4). *H. ammodendron* responded to variations in precipitation in terms of  $\Psi_L$ ; however, the  $P_s$ ,  $I_c$  and  $\Phi$  showed that photosynthetic capacity was not influenced by precipitation or soil texture (Fig. 5; Table 2). The seasonal change in  $P_s$  showed that the growth climax of *H. ammodendron* was in mid-June (Julian Days 158–173), and was not related to rainfall events or texture differences (Fig. 5a, d). However, *H. ammodendron* growing in contrasting soils showed somewhat different physiological responses to precipitation. The plants in sandy soil had consistently higher water potentials than plants of the same treatment in heavy-textured soil, indicating a generally superior water status at the sandy site (Fig. 4). At the sandy site there was a significant difference in  $\Psi_{pd}$  between no precipitation and the other two treatments ( $F = 6.47$ ,  $P = 0.003$ ), but there was no



**Fig. 4** Seasonal changes in leaf water potential of *H. ammodendron* under no precipitation (triangle with line), natural precipitation (circle with line) and double precipitation treatment (square with line) across two contrasting textured soils with two-way ANOVA ( $P = 0.05$ ) (a, b). Each value is the mean for five replications  $\pm$  SE. Error bars represent the standard error of the mean. Different lowercase letters indicate significant differences under three precipitation treatments on each day with one-way ANOVA ( $P = 0.05$ )



**Fig. 5** Seasonal changes in net photosynthetic rate at light saturation point ( $P_s$ ), apparent quantum efficiency of photosynthesis ( $\Phi$ ), and photosynthetic photon flux density at light compensation point ( $I_c$ ) of *H. ammodendron* under no precipitation (triangle with line), natural precipitation (circle with line) and double precipitation treatment (square with line) between sandy soil (a–c) and heavy-textured soil (d–f) with two-way ANOVA ( $P = 0.05$ ). Each value is the mean for five replications  $\pm$  SE. Error bars represent the standard error of the mean

significant difference between the natural precipitation and double precipitation treatments over the growing season (Fig. 4a; Table 2).  $T_r$  and WUE of *H. ammodendron* differed significantly among treatments in sandy soil ( $P < 0.001$ ) (Fig. 6a, b; Table 2), implying that gas exchange of *H. ammodendron* was affected by precipitation. However, in the heavy-textured soil, the seasonal

change of  $\Psi_{pd}$  did not differ significantly during the growing season (Fig. 4b; Table 2) among three precipitation treatments; neither did  $T_r$  and WUE among treatments (Fig. 6c, d; Table 2).

#### Above-ground biomass accumulation and root distribution

During the growing season, leaf area per branch and branch growth rate of *H. ammodendron* showed positive relationships with precipitation treatments for both soils (Fig. 7, Table 2). The climax of branch growth rate of *H. ammodendron* in both soils and all precipitation treatments was on Julian Days 158–173 in mid-June (Fig. 7b, d), which showed a strong co-occurrence with photosynthesis (Fig. 5a, d). In addition, leaf expansion and branch growth slowed down with soil water depletion at both sites; even though, in sandy soil, precipitation did not significantly influence the seasonal average of leaf area per branch and branch growth rate (Fig. 7a, b; Table 2). The branch growth rate of *H. ammodendron* in the no-precipitation treatment became negative in early August (Julian Day 214), indicating defoliation; this never occurred in the other treatments (Fig. 7b). In the heavy-textured soil, the leaf area per branch and branch growth rate significantly differed among the three treatments during the growing season ( $P = 0.05$ ) (Fig. 7c, d, Table 2). The leaf area per branch of *H. ammodendron* was less than that in sandy soil on each measuring day (Fig. 7a, c). The branch growth rate of *H. ammodendron* under no-precipitation treatment became negative in late July (Julian Day 203), earlier than for sandy soil (Fig. 7d). This showed that the absence of precipitation inhibited branch growth more severely at the heavy-textured than at the sandy site.

The vertical distribution of lateral roots under natural precipitation on contrasting soils showed different patterns. In sandy soil, the main root of *H. ammodendron* extended to an average depth of 10 m. More than 50% of feeder roots (in terms of surface area) were in the depth interval of 0–3 m (Fig. 8a). The total surface area of feeder roots was 1.7578 m<sup>2</sup> per plant (Fig. 8b). In heavy-textured soil, the main root extended to an average depth of 3.3 m, with > 50% of feeder roots (in terms of surface area) in the depth interval of 0–1 m (Fig. 8a). The surface area of feeder roots was 0.9717 m<sup>2</sup> per plant (Fig. 8b), which was only about half compared to plants at the sandy site.

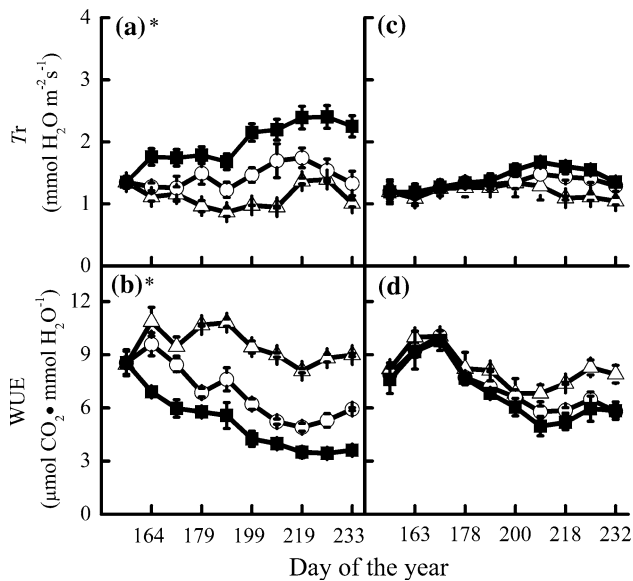
#### $\Psi_{pd}$ as an indicator of plant water status

The effects of precipitation pulses on  $\Psi_{pd}$  were detected 1 day after the precipitation (Fig. 2). The correlation between  $\Psi_{pd}$  and precipitation amount indicated a better recovery of plant water status for *H. ammodendron* in sandy soil following the same precipitation pulse compared to heavy-textured soil (Fig. 9a).  $P_s$  was not related

**Table 2** Comparison of mean physiological and growth parameters of *H. ammodendron* throughout the growing season under three precipitation treatments (none, natural, and double) at two contrasting textured soils

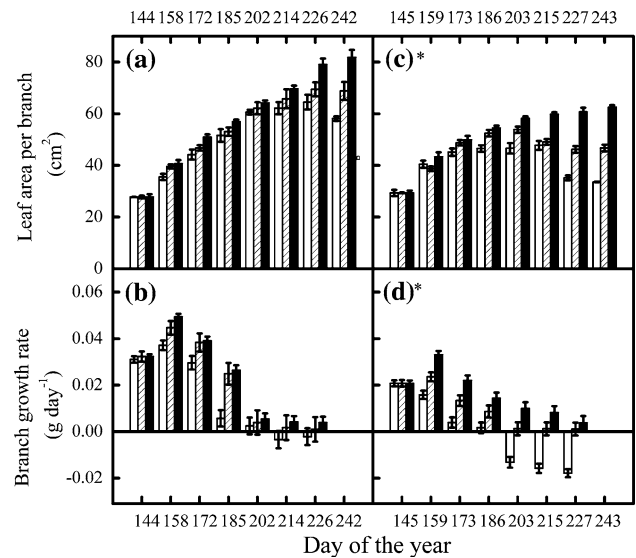
Parameters	Sandy soil			Heavy-textured soil		
	None	Natural	Double	None	Natural	Double
$\Psi_{pd}$ (MPa)	$-2.95 \pm 0.05b$	$-2.49 \pm 0.05a$	$-2.41 \pm 0.05a$	$-3.70 \pm 0.06a$	$-3.61 \pm 0.06a$	$-3.53 \pm 0.05a$
$P_s$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$9.59 \pm 0.48a$	$9.60 \pm 0.62a$	$9.59 \pm 0.48a$	$9.72 \pm 0.72a$	$9.51 \pm 0.69a$	$9.51 \pm 0.82a$
$T_r$ ( $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ )	$1.11 \pm 0.06a$	$1.44 \pm 0.14b$	$1.97 \pm 0.22c$	$1.19 \pm 0.11a$	$1.32 \pm 0.09a$	$1.41 \pm 0.07a$
WUE ( $\mu\text{mol CO}_2 \cdot \text{mmol H}_2\text{O}^{-1}$ )	$8.60 \pm 0.27a$	$6.68 \pm 0.38b$	$4.87 \pm 0.35c$	$8.15 \pm 0.42a$	$7.19 \pm 0.40a$	$6.75 \pm 0.45a$
Leaf area ( $\text{m}^2$ )	$50.56 \pm 1.57a$	$54.17 \pm 2.03a$	$58.86 \pm 1.49a$	$40.58 \pm 1.25a$	$45.64 \pm 1.04b$	$52.30 \pm 0.74c$
Branch growth rate ( $10^{-3} \text{g day}^{-1}$ )	$14.33 \pm 2.96a$	$20.97 \pm 4.21a$	$22.95 \pm 1.95a$	$0.05 \pm 1.93a$	$10.43 \pm 2.36b$	$16.76 \pm 2.23c$

Values are mean  $\pm$  SE. Values in the same half-row (for one soil) with the same letter are not significantly different at  $P = 0.05$ , and values with different letters are significantly different at  $P = 0.05$  with one-way ANOVA



**Fig. 6** Seasonal changes in maximal transpiration rate ( $T_r$ ) and photosynthetic water-use efficiency (WUE) at PPFD =  $1600 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$  for *H. ammodendron* under no precipitation (triangle with line), natural precipitation (circle with line), double precipitation treatment (square with line) at sandy soil (a, b) and heavy-textured soil (c, d) with two-way ANOVA ( $P = 0.05$ ). Each value is the mean for five replications  $\pm$  SE. Error bars represent the standard error of the mean. The asterisk (\*) indicates significant difference for each reading under three precipitation treatments with one-way ANOVA ( $P = 0.05$ )

to  $\Psi_{pd}$  at either site, indicating stable carbon assimilation (on a leaf area basis) independent of plant water conditions (Fig. 9b). The branch growth rate increased with  $\Psi_{pd}$  in both soils through all precipitation treatments. *H. ammodendron* at the sandy site experienced better water conditions throughout the growing season, which ensured a higher growth rate under the same precipitation treatment compared to heavy-textured soil (Fig. 9c). The weaker relationship between  $\Psi_{pd}$  and branch growth rate in sandy soil ( $R^2 = 0.57$ ) indicated that growth was less restricted than in heavy-textured soil. The negative relationship between WUE and  $\Psi_{pd}$  indicated the WUE of *H. ammodendron* increased under water stress at either site. The stronger relationship



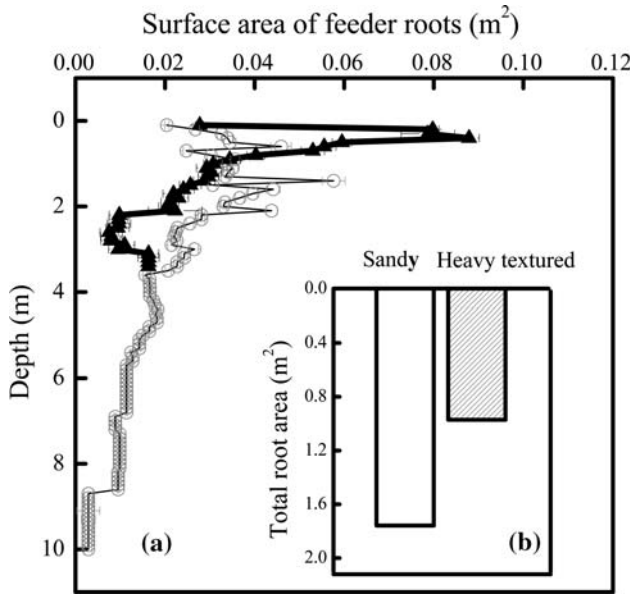
**Fig. 7** Seasonal changes in leaf area per branch and growth rate of branch biomass of *H. ammodendron* under no precipitation (open rectangle), natural precipitation (hashed rectangle), and double precipitation treatment (closed rectangle) in sandy soil (a, b) and heavy-textured soil (c, d) with two-way ANOVA ( $P = 0.05$ ). Each value is the mean for five replications  $\pm$  SE. Error bars represent the standard error of the mean. The asterisk (\*) indicates significant difference for each reading under three precipitation treatments with one-way ANOVA ( $P = 0.05$ )

between WUE and  $\Psi_{pd}$  at the sandy site ( $R^2 = 0.85$ ) indicated a much larger buffering capability against wetting–drying events for *H. ammodendron* at this site (Fig. 9d).

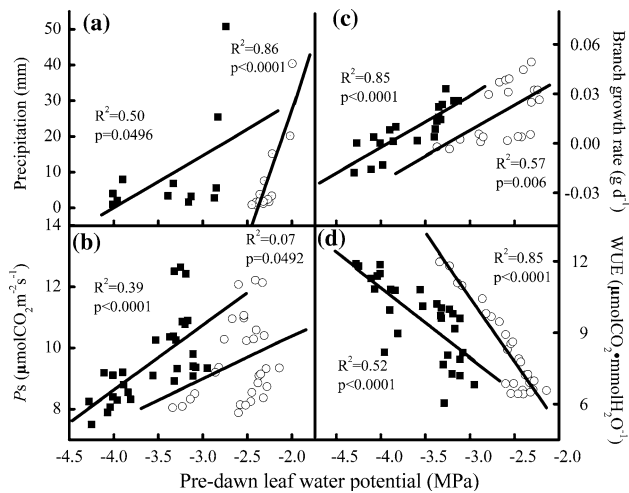
## Discussion

How does *H. ammodendron* respond to precipitation pulses at contrasting textured soils?

On the basis of basic plant physiology, we might expect *H. ammodendron* to respond strongly to occasional rainfall or sustained drought. Contrary to such a prediction, there was no significant photosynthetic response to large summer pulse or sustained drought during the season in



**Fig. 8** Root distribution of *H. ammodendron* in sandy soil (circle with line) and heavy-textured soil (triangle with line) at the end of the natural precipitation treatment. **a** Vertical distribution of feeder roots throughout the soil profile across two contrasting soil textures at the end of the natural precipitation treatment; **b** the total feeder root area across two contrasting soil textures at the end of the natural precipitation treatment. Error bars represent the standard error of the mean



**Fig. 9** Correlation between pre-dawn leaf water potential ( $\Psi_{pd}$ ) of *H. ammodendron* and related factors in sandy soil (circle) and heavy-textured soil (square) during the growing season. **a** Correlation between  $\Psi_{pd}$  and precipitation (mm). **b** Correlation between photosynthetic rate at light saturation point ( $P_s$ ) and  $\Psi_{pd}$  of both soils. **c** Correlation between branch growth rate and  $\Psi_{pd}$  of both soils. **d** Correlation between photosynthetic water use efficiency (WUE) and  $\Psi_{pd}$  of both soils. The data from three treatments are all plotted. PPF: photosynthetic photo flux density

either soil (Figs. 3, 5; Table 2). Typical photosynthetic characteristics of  $C_4$  species (Pyankov et al. 1999) were shown by *H. ammodendron*, such as a lower  $\Phi$  at low PPF, higher  $I_c$  (Fig. 5a–f), which all contributed to its

strong xeromorphic features. The consistency of  $I_c$  and  $\Phi$  during the growing season indicated that its photosynthetic activities were maintained at a stable high level within a wide range of  $\Psi_L$  from  $-5.68$  to  $-2.54$  MPa (Figs. 2, 4, 9). Xu et al. (2007) reported that such photosynthetic consistency was achieved either by strategic adaptation in water use, or by integrated physiological and morphological regulations. It has been suggested that, over the short term, drought has a substantial impact on gas exchange (Schulze 1993), and over the long term, structural changes could alleviate the direct effects of water stress on gas exchange (Geiger and Servaites 1991). Under natural precipitation, the seasonal fluctuation in  $P_s$  showed the growth climax in mid-June (Julian Days 158–173) for both soils (Fig. 5a, d), which agreed with the latter assertion.

Significant differences in soil texture can account for the apparent discrepancy in SMC reported here (Hacke et al. 2000; Hennessy et al. 1985; Noy-Meir 1973) (Fig. 1). Van de Griend and Owe (1994) suggested that while coarse-textured soils dry out quickly during the constant rate phase of evaporation, resistance to evaporation increases quickly as pore spaces dry out. Therefore, evaporation rates in coarse soils may be surpassed by evaporation rates of finer soils that are still evaporating via water conduction (Philip 1957). Not surprisingly, the heavy-textured soil with higher evaporation rate limited infiltration of moisture inputs during summer, thus reducing the effectiveness of a large rain pulse (Xu and Li 2008), which was clearly demonstrated by the effect of rainfall on  $\Psi_{pd}$  (Fig. 9a). In fact, after the large rain pulse, both  $\Psi_{pd}$  and  $\Psi_m$  decreased more rapidly in heavy-textured than sandy soil (Fig. 2).

Theory predicts that coarse-textured soils hold water less tightly (with less negative matrix potential) than finer-textured soils (Noy-Meir 1973). Thus, plants growing in sandy soils require less negative water potential to extract water than plants in a loam or finer soil (Hacke et al. 2000; Sperry and Hacke 2002). We showed that plants growing in sandy soil had consistently higher water potentials than plants under the same treatment in heavy-textured soil, which supports those assertions. The negative correlation between WUE and  $\Psi_{pd}$  in both soils (Fig. 9d) showed that high sensitivity to soil moisture availability ensured increased WUE under water stress. At the sandy site,  $T_r$  and WUE of *H. ammodendron* appeared to be highly sensitive to a large precipitation pulse and differed significantly between precipitation treatments during the growing season (Fig. 6a, b; Table 2). When water is plentiful, decreased WUE associated with high  $T_r$  can be adaptive (Donovan and Ehleringer 1992). The lower WUE after the large summer precipitation pulse and under double precipitation suggested a lack of tight stomatal control under favorable water conditions (Fig. 6b, Table 2). Overall,  $\Psi_L$ ,  $T_r$ , and WUE of *H. ammodendron* all depended on precipitation. However, at the heavy-textured site, the  $\Psi_L$ ,  $T_r$ , and WUE were not significantly affected by precipitation over the season (Figs. 4b, 6c, d; Table 2),



indicating the limited water availability in fine-textured soil. Moreover, WUE in the heavy-textured site for both natural and double precipitation treatments were higher than those in sandy soil, which indicated that increased WUE conserved water (Heschel and Hausmann 2001; Heschel et al. 2004; Zangerl and Bazzaz 1984).

### Importance of morphological adaptation

There are a wide variety of morphological, anatomical, and physiological characteristics that either serve as adaptations or act to buffer plants against the damaging effects of water deficits. The balance between water supply and demand in a plant can be maintained by morphological adjustment of shoot and root systems, as found in some small tree species (Donovan and Ehleringer 1994). In our case, *H. ammodendron* obviously also benefited from effective morphological adjustment, in which both defoliation and the root system adjustment acted effectively to maintain photosynthetic stability (Figs. 3, 7, 8). However, the effectiveness/sensitivity of this morphological adjustment was obviously not the same for the two sites. In sandy soil, when  $\Psi_{pd} < -3.0$  MPa, the assimilative organ defoliated (Fig. 9c, when branch growth rate  $< 0$ ). In heavy-textured soil, *H. ammodendron* had less leaf area per branch to reduce the transpiring surface, and defoliation occurred until  $\Psi_{pd} < -3.75$  MPa (Fig. 9c, when branch growth rate  $< 0$ ). The higher sensitivity of branch growth to  $\Psi_{pd}$  at sandy site indicated a more effective morphological adjustment to water conditions, which is also partially responsible for the better plant water status at this site (Figs. 2, 4).

Plants can acclimate to different environments through modifying the amount or distribution of roots to maintain its regular activities (Li et al. 2005). The root system develops in accordance with a species-specific morphological pattern and to the extent that local conditions permit (Larcher 2003). Although plants in sandy soil can access water with higher leaf water potentials, they may also require deeper roots in a drought-prone habitat than plants in finer soils (Hacke et al. 2000). *H. ammodendron* developed more feeder roots in sandy compared to heavy-textured soil (Fig. 8), showing that plants at coarse soils have a greater need to develop more roots. Functionally, plants that have greater water acquisition potential from high biomass allocation to roots may not require increased WUE to persist in drought conditions. Conversely, plants that allocate less biomass to roots might require higher WUE in persistent drought conditions because of the lower water acquisition capacity of the smaller root surface areas (Griffith et al. 2004).

### Conclusions

This is an integrated research on detailed physiological response to precipitation and morphological character-

istics in contrasting textured soils of *H. ammodendron*. These results indicate that the selective use of physiological and morphological modes of stress response may reflect a compensatory relationship among traits. *H. ammodendron* coped with changes in precipitation at given soil hydraulic characteristics, chiefly through effective morphological adjustment combined with appropriate physiological responses. The active acclimation induced by special environmental conditions formed the foundation of buffering ability against extreme environmental variations; this buffering capacity is stronger for *H. ammodendron* growing at a sandy site than at a heavy-textured site. As dominated species in desert control both the overall biomass and primary productivity of the desert ecosystem, its good performance will, to a great extent, determine the better future of the desert ecosystem at sandy site.

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### References

- Cheng XL, An SQ, Li B, Chen JQ, Lin GH, Liu YH, Luo YQ, Liu SR (2006) Summer rain pulse size and rainwater uptake by three dominant desert plants in a desertified grassland ecosystem in northwestern China. *Plant Ecol* 184:1–12. doi:10.1007/s11258-005-9047-6
- Chesson P, Gebauer RLE, Schwinning S, Huntly N, Wiegand K, Ernest MSK, Sher A, Novoplansky A, Weltzin JF (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141:236–253. doi:10.1007/s00442-004-1551-1
- Cohen Y, Li Y (1996) Validating sap flow measurement in field-grown sunflower and corn. *J Exp Bot* 47:1699–1707
- Cohen Y, Fuchs M, Falkenflug V, Moreshet S (1988) Calibrated heat pulse method for determining water uptake in cotton. *Agron J* 80:398–402
- Donovan LA, Ehleringer JR (1992) Contrasting water-use patterns among size and life-history classes of a semi-arid shrub. *Funct Ecol* 6:482–488
- Donovan LA, Ehleringer JR (1994) Water stress and use of summer precipitation in a Great Basin shrub community. *Funct Ecol* 8:289–297
- Dougherty RL, Lauenroth WK, Singh JS (1996) Response of a grassland cactus to frequency and size of rainfall events in a North American shortgrass steppe. *J Ecol* 84:177–183
- Dube OP, Pickup G (2001) Effects of rainfall variability and communal and semi-commercial grazing on land cover in southern African rangelands. *Clim Res* 17:195–208. doi:10.3354/cr017195
- Ehleringer JR, Schwinning S, Gebauer R (1999) Water use in arid land ecosystems. In: Press MC, Scholes JD, Barker MG (eds) *Physiological plant ecology*. Blackwell Science, Boston, pp 347–365
- Fahn A, Cutler DF (1992) Xerophytes. *Handbuch der Pflanzenanatomie, Spezieller Teil, Band XIII, Teil 3*. Gebrüder Borntraeger, Berlin
- Flanagan LB, Ehleringer JR, Marshall JD (1992) Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant Cell Environ* 15:831–836

- Fravolini A, Hultine KR, Koepke DF, Williams DG (2003) The role of soil texture on mesquite water relations and response to summer precipitation. In: Santa Rita experimental range: 100 years of accomplishment and contributions, conference proceedings, Tucson, Arizona, USA. Proceedings RMRS-P-30, pp 125–129. (USDA Forest Service, Rocky Mountain Research Station: Tucson, AZ, USA)
- Fravolini A, Hultine KR, Brugnoli E, Gazal R, English NB, Williams DG (2005) Precipitation pulse use by an invasive woody legume: the role of soil texture and pulse size. *Oecologia* 144:618–627. doi:10.1007/s00442-005-0078-4
- Geiger DR, Servaites JC (1991) Carbon allocation and response to stress. In: Mooney HA, Winner WE, Pell EJ (eds) Response of plants to multiple stresses. Academic Press, San Diego, pp 103–127
- Golluscio RA, Sala OE, Lauenroth WK (1998) Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia* 115:17–25. doi:10.1007/s004420050486
- Griffith C, Kim E, Donohue K (2004) Life-history variation and adaptation in the historically mobile plant *Arabidopsis thaliana* (Brassicaceae) in North America. *Am J Bot* 91:837–849
- Hacke UG, Sperry JS, Ewers BE, Ellsworth DS, Schafer KVR, Oren R (2000) Influence of soil porosity on water use in *Pinus raeda*. *Oecologia* 124:495–505. doi:10.1007/PL00008875
- Hamerlynck EP, McAuliffe JR, McDonald EV, Smith SD (2002) Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. *Ecology* 83:768–779. doi:10.1890/0012-9658(2002)083[0768:EROTMD]2.0.CO;2
- Hamerlynck E, Huxman T, McAuliffe J, Smith S (2004) Carbon isotope discrimination and foliar nutrient status of *Larrea tridentata* (creosote bush) in contrasting Mojave Desert soils. *Oecologia* 138:210–215. doi:10.1007/s00442-003-1437-7
- Hennessy JT, Gibbens RP, Tromble JM, Cardenas M (1985) Mesquite (*Prosopis glandulosa* Torr.) dunes and interdunes in southern New Mexico: a study of soil properties and soil water relations. *J Arid Environ* 9:27–38
- Heschel MS, Hausmann NJ (2001) Population differentiation for abscisic acid responsiveness in *Impatiens capensis* (Balsaminaceae). *Int J Plant Sci* 162:1253–1260. doi:10.1086/322951
- Heschel MS, Sultan SE, Glover S, Sloan D (2004) Population differentiation and plastic responses to drought stress in the generalist annual *Polygonum persicaria*. *Int J Plant Sci* 165:817–824. doi:10.1086/421477
- Huang ZY, Wu H, Hu ZH (1997) The structures of 30 species of psammophytes, and their adaptation to the sandy desert environment in Xinjiang (in Chinese). *Acta Phytoecol Sin* 21:521–530
- Huang ZY, Zhang XS, Zheng GH, Gutterman Y (2003) Influence of light, temperature, salinity and storage on seed germination of *Haloxylon ammodendron*. *J Arid Environ* 55:453–464. doi:10.1016/S0140-1963(02)00294-X
- Hultine KR, Koepke DF, Pockman WT, Fravolini A, Sperry JS, Williams DG (2006) Influence of soil texture on hydraulic properties and water relations of a dominant warm-desert phreatophyte. *Tree Physiol* 26:313–323
- Huxman TE, Cable JM, Ignace DD, Eilts JA, English NB, Weltzin J, Williams DG (2004) Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141:295–305. doi:10.1007/s00442-003-1389-y
- Kripalani RH, Oh JH, Chaudhari HS (2007) Response of the East Asian summer monsoon to doubled atmospheric CO<sub>2</sub>: coupled climate model simulations and projections under IPCC AR4. *Theor Appl Climatol* 87:1–28. doi:10.1007/s00704-006-0238-4
- Larcher W (2003) Water uptake by roots. In: Physiological plant ecology: ecophysiology and stress physiology of functional groups, 4th edn. Springer, Berlin Heidelberg New York, pp 225–229
- Li Y, Xu H, Cohen S (2005) Long-term hydraulic acclimation to soil texture and radiation load in cotton. *Plant Cell Environ* 28:492–499. doi:10.1111/j.1365-3040.2005.01291.x
- Loik ME (2007) Sensitivity of water relations and photosynthesis to summer precipitation pulses for *Artemisia tridentata* and *Purshia tridentata*. *Plant Ecol* 191:95–108. doi:10.1007/s11258-006-9217-1
- McAuliffe JR (1994) Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert Bajadas. *Ecol Monogr* 64:111–148. doi:10.2307/2937038
- Meinzer FC (2002) Co-ordination of vapor and liquid phase water transport properties in plants. *Plant Cell Environ* 25:265–274
- Nilsen ET, Orcutt DM (1996) The physiology of plants under stress: soil and biotic factors. Wiley, New York
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Ann Rev Ecol Syst* 4:25–51. doi:10.1146/annurev.es.04.110173.000325
- Philip JR (1957) Evaporation, and moisture and heat fields in the soil. *J Atmos Sci* 14:354–366. doi:10.1175/1520-0469(1957)014<0354:EAMAHF>2.0.CO;2
- Phillips SL, Ehleringer JR (1995) Limited uptake of summer precipitation by bigtooth maple (*Acer grandidentatum* Nutt) and Gambel's oak (*Quercus gambelii* Nutt). *Trees-Struct Funct* 9:214–219. doi:10.1007/BF00195275
- Pyankov VI, Black CC, Artyusheva EG, Voznesenskaya EV, Ku MSB, Edwards GE (1999) Features of photosynthesis in Haloxylon species of Chenopodiaceae that are dominant plants in central Asian deserts. *Plant Cell Physiol* 40:125–134
- Sage RF (1994) Acclimation of photosynthesis to increasing atmospheric CO<sub>2</sub>: the gas exchange perspective. *Photosynth Res* 39:351–368
- Sala OE, Lauenroth WK, Golluscio RA (1997) Plant functional types in temperate semi-arid regions. In: Smith TM, Shugart HH, Woodward FI (eds) Plant functional types. Cambridge University Press, Cambridge, pp 217–233
- Schlesinger WH, Pilmanis AM (1998) Plant–soil interactions in deserts. *Biogeochemistry* 42:169–187. doi:10.1023/A:1005939924434
- Schulze ED (1993) Soil water deficits and atmospheric humidity as environmental signals. In: Smith JAC, Griffiths H (eds) Water deficits: plant response from cell to community. Bios Scientific Publishers, Oxford, pp 129–145
- Schwinning S, Starr BI, Ehleringer JR (2003) Dominant cold desert plants do not partition warm season precipitation by event size. *Oecologia* 136:252–260. doi:10.1007/s00442-003-1255-y
- Sperry JS, Hacke UG (2002) Desert shrub water relations with respect to soil characteristics and plant functional type. *Funct Ecol* 16:367–378. doi:10.1046/j.1365-2435.2002.00628.x
- Sultan SE, Wilczek AM, Hann SD, Brosi BJ (1998) Contrasting ecological breadth of co-occurring annual *Polygonum* species. *J Ecol* 86:363–383. doi:10.1046/j.1365-2745.1998.00265.x
- van de Griend AA, Owe M (1994) Bare soil surface resistance to evaporation by vapor diffusion under semiarid conditions. *Water Resour Res* 30:181–188
- Whitford WG (2003) Ecology of desert systems. *J Mammal* 84:1122–1124. doi:10.1644/1545-1542(2003)084<1122:EODS>2.0.CO;2
- Wu ZY (1980) Vegetation of China (in Chinese). Science Press, Beijing, pp 1–1144
- Xu H, Li Y (2006) Water-use strategy of three central Asian desert shrubs and their responses to rain pulse events. *Plant Soil* 285:5–17. doi:10.1007/s11104-005-5108-9
- Xu GQ, Li Y (2008) Rooting depth and leaf hydraulic conductance in the xeric shrub *Haloxylon ammodendron* growing at sites of contrasting soil texture. *Funct Plant Biol* 35:1234–1242. doi:10.1071/FP08175
- Xu H, Li Y, Xu GQ, Zou T (2007) Ecophysiological response and morphological adjustment of two Central Asian desert shrubs towards variation in summer precipitation. *Plant Cell Environ* 30:399–409. doi:10.1111/j.1365-3040.2006.001626.x
- Zangerl AR, Bazzaz FA (1984) Effects of short-term selection along environmental gradients on variation in populations of *Amaranthus retroflexus* and *Abutilon theophrasti*. *Ecology* 65:207–217