South African Journal of Botany 92 (2014) 53-58



Contents lists available at ScienceDirect

# South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

# Soil water threshold for the growth of *Haloxylon ammodendron* in the Ulan Buh desert in arid northwest China



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## ARTICLE INFO

Article history: Received 10 October 2013 Received in revised form 4 January 2014 Accepted 5 February 2014 Available online 6 March 2014

Edited by JF Rivas

Keywords: Water potential Aeolian soil water content Transpiration rate Economic water threshold Survival water threshold

# ABSTRACT

An experiment was conducted over a 3-year period to investigate the aeolian soil water dynamics and ecophysiological characteristics of *Haloxylon ammodendron* in Ulan Buh Desert, northwest China. Three different communities of *H. ammodendron*, which consist of two 8- to 10-year plantations and one natural stand, were selected in this study. As a result, the "economic water threshold" of *H. ammodendron* was expressed at about 2.0% of the absorbed water content. Above this threshold, the aeolian soil water potential decreased by -0.18 MPa with a 1.0% decrease in the water content. Below this threshold, the aeolian soil water potential decreased by -2.09 MPa with a 1.0% decrease in the water content. The predawn water potential of the shoot can recover to an above zero turgor pressure when the aeolian soil water content exceeded the "economic water threshold". However, the predawn water potential of the shoot became -3.50 MPa, which was lower than that at zero turgor (-3.41 MPa) when the aeolian soil water content was about 1.0%. This results indicated that the shoot cannot recover its turgor. Therefore, 1.0% of the aeolian soil water content was defined as the "survival water threshold" of the growth of *H. ammodendron*.

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# 1. Introduction

*Haloxylon ammodendron*, a large shrub in the Chenopodiaceae family, is naturally distributed in deserts, including sandy, gravel, clay, and salt desert. This shrub often forms a large area of pure stand in some deserts. *H. ammodendron* is an important sand-fixing shrub and could also be used as firewood (Wu, 1979). The shrub is a dominant species of the desert vegetation in China and is mainly distributed in the Xinjiang Autonomous Region, Inner Mongolia Autonomous Region, Qinghai Province and Gansu Province (Liu et al., 2011).

Previous ecophysiological studies on *H. ammodendron* mainly focused on 2 aspects. (1) Physiological studies such as photosynthesis regulation under different water conditions (Su et al., 2007), stem sap flow and water consumption under drip irrigation (Xu et al., 2008), canopy and leaf gas exchange in different soil water conditions (Gao et al., 2010), response of chlorophyll *a* fluorescence to the irrigation of saline groundwater (Han et al., 2010), response of photosynthesis and water potential to precipitation (Zou et al., 2010), vegetation dynamics and soil carbon and nitrogen accumulation under controlled grazing (Zhou et al., 2011), and fertile island and lower pH and EC induced by stem flow (Li et al., 2011). (2) Growth studies such as the crown and root growth in hinterland of desert (Wei et al., 2007), growth and biomass allocation in different irrigation conditions (Shan et al., 2008), and genetic variation of seed germination and seedling traits (Liu et al., 2011). However, one of the most important factors for the growth of *H. ammodendron* in the desert is the threshold of water availability, especially in aeolian soil water conditions.

*H. ammodendron* was widely used as part of the desertification control projects of China and as one of the dominant shrubs in the shelter belt to control desertification in the Ulan Buh desert since the 1980s. However, some *H. ammodendron* plantations degraded, where the assimilating shoot becomes yellow and withers during the summer drought. High mortality recently occurred for the *H. ammodendron*. The main water source of *H. ammodendron* is soil water because of low and unpredictable rainfall. However, we still do not know the aeolian soil water conditions for the growth of *H. ammodendron*. Therefore, we selected a mature *H. ammodendron* plantation and its natural community to study the changes in the physiological and ecological characteristics of the *H. ammodendron* in response to the aeolian soil moisture

Table 1	
Characteristics of the 3 kinds of communities of <i>H. ammodendron</i> .	

Туре	Density (plant h <sup>-1</sup> )	Height (cm)	Ground water table (m)
8- to10-year plantation (No. 1)	$1800\pm72$	$230\pm56$	6.2
8- to 10-year plantation (No. 2)	$2420\pm96$	$210\pm34$	5.2
Natural stand (No. 3)	$830\pm46$	$220\pm43$	6.7

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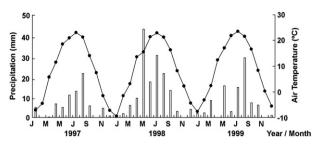


Fig. 1. Monthly precipitation (bars) and air temperature (points) in the Ulan Buh Desert during the field experiment (January 1997 to December 1999).

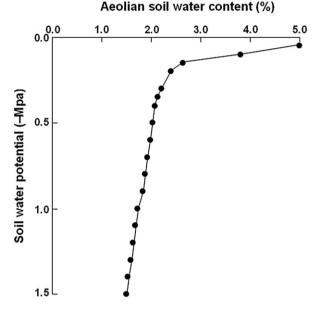


Fig. 2. Relationship between the water potential and water content of aeolian soil.

in the Ulan Buh Desert. We aim to examine the suitable and minimal aeolian soil water conditions for the growth of *H. ammodendron*.

# 2. Material and methods

# 2.1. Site characteristics

Field experiments were conducted in the Dengkou Combating Desertification Bureau of Experimental Center ( $40^{\circ}28'$  N,  $106^{\circ}46'$  E) in the northeast edge of the Ulan Buh Desert, northwest China, with an elevation of 1050 m to 1060 m. The site is a temperate arid climate zone with a mean annual precipitation of 152.7 mm. The mean potential evaporation is 2351 mm, which is over 15 times that of the mean annual precipitation. The mean annual air temperature is 7.5 °C with a maximum of 38.7 °C in July and a minimum of -32.8 °C in January. The climate is dry, windy, and hot in the summer and cold in the winter. The dominant vegetation type is the shrub, including *Nitraria tangutorum*, *Artemisia ordosica*, *Artemisia sphaerocephala*, and *H. ammodendron*. Most of the vegetation is found in the lower part of the sand dune and in the interdune. The vegetation coverage varies from 10% to 30%.

*H. ammodendron* grows on 3 m to 5 m high dunes formed by the alluvial deposits of the Yellow River after the wind blows. The soil of the

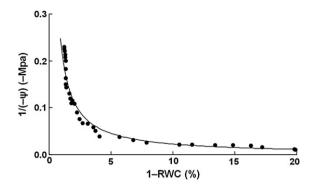


Fig. 3. P–V curve of *H. ammodendron*. RWC: relative water content.  $\psi$ : water potential.

sand dunes is aeolian with a diameter of 0.05 mm to 0.25 mm for most soil (80% to 90%) in the aeolian soil on the sand dunes. The bulk density of the aeolian soil is 1.60 to 1.70 (g cm<sup>-3</sup>). Three different communities of *H. ammodendron*, comprising two 8- to 10-year plantations (Nos. 1 and 2, respectively) and one natural stand (No. 3), were selected based on the extensive investigations of the soil moisture across the distribution area of *H. ammodendron* in the Ulan Buh. Mobile sand dunes without any plantation were chosen as the control. The details of the characteristics of the selected communities are shown in Table 1.

# 2.2. Measurement of soil water conditions

The aeolian soil water potential was measured from May to September 1997 using a *HR*-33*T* dewpoint potentiometer (*Wescor Company*, Logan, UT, USA). The soil samples were collected at 0, 10, 20, 40, 60, 80, 100, 120, 150, and 200 cm depths with 3 replicates. The soil samples were dried at 105 °C for 12 h. The aeolian soil water content was calculated using the equation as follows:

Aeolian soil water content (%) =  $\frac{\text{wet soil weight} - \text{dry soil weight}}{\text{dry soil weight}} \times 100\%.$ 

# 2.3. Measurement of water status of H. ammodendron

The pressure–volume (P–V) curve for the *H. ammodendron* shoots was constructed through the Hammel method (Tyree and Hammel, 1972). The water potential of the assimilating shoot of the *H. ammodendron* in the 3 plots was measured from May to September 1997 using a *PMS* 600 pressure chamber (*Corvallis Company*, OR, USA). The daily dynamics of the transpiration rate (*E*) of *H. ammodendron* in natural community was measured by a *Li-1600* porometer (*LI-COR Inc.*, Lincoln, Nebraska, USA) on five sunny days from July to August 1998. The daily dynamics of the *E* of the assimilating shoot of the 8- to 10-year *H. ammodendron* plantations was measured 2 to 5 times every month during the growing season (July to August) in 1999.

### 2.4. Statistical analysis

The measurements were performed 5 times for the aeolian soil water potential, water potential, and E of the assimilating shoot of *H. ammodendron*. The means and calculated standard error (SE) are reported.

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 $\psi_x^0$  and  $\psi_x^{100}$  of the growing period of *H. ammodendron* from June to September 1997 (n = 5).

Months	June	July	August	September	Mean
$\psi_{\rm x}^0$ (Mpa)	$-3.36 \pm 0.12$	$-3.39\pm016$	$-3.42\pm0.06$	$-3.46\pm0.09$	$-3.41 \pm 0.11$
$\psi_{\rm x}^{100}$ (Mpa)	$-2.72 \pm 0.08$	$-2.79 \pm 013$	$-2.86 \pm 0.08$	$-2.92 \pm 0.11$	$-2.82 \pm 0.10$

Table 3	3
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Water potential (mean  $\pm$  SE) of the assimilating shoot of *H. ammodendron* in different aeolian soil water moisture (n = 5).

Туре	8- to 10-year plantation (No. 1)	8- to 10-year plantation (No. 2)	Natural community (No. 3)
Mean aeolian soil water content (%)	$1.12 \pm 0.23$	0.98 ± 0.16	$2.69\pm0.19$
Mean aeolian soil water potential (MPa)	$-1.36 \pm 0.15$	$-2.40 \pm 0.24$	$-0.28 \pm 0.11$
Mean daily water potential of shoot (MPa)	$-4.13 \pm 0.41$	$-4.58 \pm 0.37$	$-3.35 \pm 0.29$
Predawn water potential of shoot (MPa)	$-2.55 \pm 0.24$	$-3.65 \pm 0.29$	$-1.60 \pm 0.16$
Minimal daily water potential of shoot (MPa)	$-4.70 \pm 0.25$	$-5.00 \pm 0.39$	$-4.50\pm0.31$

# 3. Results

3.1. Monthly precipitation and air temperature in Ulan Buh Desert from 1997 to 1999

From January 1997 to December 1999, the mean monthly air temperature ranged from -9.5 °C in January to 23.5 °C in July. The mean annual air temperatures in 1997, 1998, and 1999 were 8.5 °C, 9.1 °C, and 8.9 °C, respectively, and the annual precipitations were 78.2, 159.7, and 96.1 mm, respectively. The mean monthly precipitation ranged from 0.0 mm in February 1997 to 45.4 mm in May 1998 (Fig. 1).

# 3.2. Characteristics of aeolian soil water potential

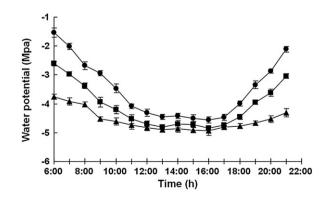
The relationship between the water content ( $\omega$ ) and the water potential ( $\psi_s$ ) of the aeolian soil was as follows:

$$\psi_{\rm s} = -10.91944 \times 0.25559^{\omega} \ \left(R^2 = 0.9997\right). \tag{1}$$

The aeolian soil water content and soil water potential at the curve inflection point were 2.0% and -0.72 MPa, respectively (Fig. 2).

# 3.3. The P-V curve of H. ammodendron

The  $\psi_x^{100}$  (water potential of the assimilating shoot at a saturated turgor) and  $\psi_x^0$  (water potential of the assimilating shoot at zero turgor) of the *H. ammodendron* growth phase were determined by the P–V curves (Table 2). The mean water parameters of the *H. ammodendron* were  $\psi_x^{100} = -2.82$  MPa,  $\psi_x^0 = -3.41$  MPa, RWD<sup>0</sup> = 10% (relative water deficit at zero turgor),  $V_s = 0.35$  (free water content),  $Va \cdot Vs^{-1} = 1.86$  (ratio of bound and free water content), and  $\epsilon_{max} = -8.4$  (maximum volumetric elastic modulus). The turgor of the assimilating shoot disappeared when the relative water deficit was 10.53%. However, the osmotic potential at a zero point of turgor was as low as -3.41 MPa (Fig. 3).

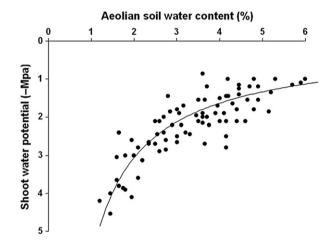


**Fig. 4.** Water potential of the assimilating shoot of Nos. 2 (triangles), 1, (squares), and 3 (points) of *H. ammodendron* in 1998 (n = 5). The mean aeolian soil water content of Nos. 2, 1, and 3 of *H. ammodendron* were 0.98%, 1.12%, and 2.69%, respectively.

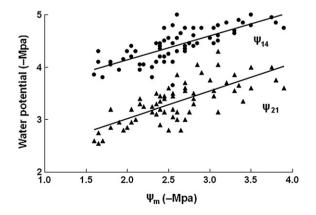
3.4. The relationship of the water potential of the assimilating shoot and aeolian soil water content

The daily means of the water potential of the assimilating shoot of *H. ammodendron* were -3.35, -4.13, and -4.58 MPa when the aeolian soil water content decreased by 2.69% and 1.12% to 0.98% (Table 3). The water potential of the assimilating shoot decreased with the drought stress (Nos. 1 and 2, respectively). The predawn water potential decreased by 59% and 128%, and the midday water potential (minimum) was decreased by 4% and 11%, respectively (compare with No. 3). The daily range of the water potential of the assimilating shoot decreased by about 26% and 50%, Nos. 1 and 2 respectively, in the lower aeolian soil water content conditions (Fig. 4).

When the characteristic curve of the water potential of aeolian soil is shown in Eq. (1), the relationship between the predawn water potential



**Fig. 5.** Relationship of the predawn water potential of the assimilating shoot of *H. ammodendron* (06:00) and the aeolian soil water content during the growing season (May to September) of 1997.



**Fig. 6.** Relationship among predawn  $(\psi_m)$ , midday  $(\psi_{14})$ , and evening  $(\psi_{21})$  water potential of the assimilating shoot of *H. ammodendron* during the growing season (May to September) of 1997.

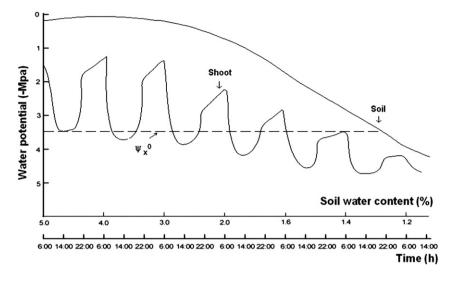


Fig. 7. Relationship between the daily dynamics of the water potential of the assimilating shoot of *H. ammodendron* and aeolian soil water content. The dashed horizontal line is the water potential of the assimilating shoot at zero turgor.

 $(\psi_m)$  of H. ammodendron and the aeolian soil water content  $(\omega)$  is shown as

$$\psi_m = 1.02332 \times e^{1.4759 \omega^{-1}} \ \Big( R^2 = 0.9997 \Big). \eqno(2)$$

The predawn water potential of the assimilating shoot of *H. ammodendron* was about -2.82 MPa, and the relevant aeolian soil water content was 2.0% (Fig. 5).

The relationship among the predawn  $(\psi_m)$ , midday  $(\psi_{14})$  and evening  $(\psi_{21})$  water potential of the assimilating shoot is shown in Fig. 6. The equations are as follows:

$$\psi_{14} = 3.04282 + 0.53087 \times \psi_m \ (r = 0.9102) \eqno(3)$$

$$\psi_{21} = 1.41708 + 0.723162 \times \psi_m \ (r = 0.9881). \tag{4}$$

The equation could similarly be regressed at other times. These equations could be used to simulate the water potential of the assimilating shoot at any time of 1 day and in different aeolian soil water contents.

#### Table 4

Aeolian soil moisture under different growth types of Haloxylon ammodendron.

Therefore, the daily dynamics of the water potential of an assimilating shoot and the aeolian soil water content could be simulated through their relationship (Fig. 7). Our data indicated that the predawn water potential of an assimilating shoot of *H. ammodendron* could not recover to the same level as that of the aeolian soil even with high soil water availability. The water potential of the shoot also dramatically reduced in the afternoon around 14:00 and often appeared lower than  $\psi_x^0$  in the potential evaporation during sunny weather.

# 3.5. The relationship of the aeolian soil water content and the growth of *H. anmodendron*

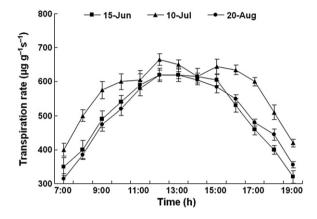
The plant growth and the aeolian soil moisture were simultaneously long-term monitored for the different growth conditions of *H. ammodendron* in the Ulan Buh regions (Table 4). The results revealed that *H. ammodendron* grows well when the aeolian soil water content is basically maintained at 2.0%. All *H. ammodendron* with recession features in growth were in an aeolian soil water content of less than 2.0%. The stand severely degraded when the aeolian soil water content is below 1.0%.

Growth status	Survey site	Date	Depth of	Aeolian soil	moisture(%)	Forest-type	Growth situation	
			underground water	0–40 (cm)	40-200 (cm)		Height (m)	Situation description
Normal	South of Zong He forest farm, Ming Qin	Aug.	6.9	$1.5\pm0.13$	$2.6\pm0.31$	Man-plant	$2.1\pm0.20$	Green crown, growth prosperity
	JiLantai, Inner Mongolia	Aug.	6.5	$1.7\pm0.58$	$3.4\pm0.69$	Natural	$2.6\pm0.34$	Green crown, growth prosperity
	Lin Zhe Combanting Station	Aug.	6.0	$1.1\pm0.35$	$2.2\pm0.43$	Man-plant	$2.3\pm0.22$	Green crown, growth prosperity
	DengKou, Inner Mongolia	Aug.	7.7	$1.3\pm0.23$	$2.8\pm0.51$	Man-plant	$3.0\pm0.27$	Most of leaf being green growth prosperity
Degeneration	East of Deng Kou Combating Desertification Bureau of Arboretum	July	6.0	$0.6\pm0.14$	$1.1\pm0.22$	Man-plant	$1.7\pm0.27$	Under middle of leaf being yellow, tree crown decreasing
	West-north of Min Qin Combating Station	July	6.6	1.1 ± 0.09	$1.3\pm0.24$	Man-plant	$2.0\pm0.13$	Under middle of leaf converting yellow
	West-north Lin Zhe Combanting Station	July	9.0	$0.8\pm0.13$	$1.3\pm0.20$	Man-plant	$1.5\pm0.12$	Under middle of leaf being yellow
	North of Lin Zhe Combanting Station	July	8.0	0.9 ± 0.11	$1.4\pm0.22$	Man-plant	$1.6\pm0.13$	Under middle of leaf converting yellow
	South of Zong He forest farm, Ming Qin	Aug.	6.9	$1.1\pm0.08$	$1.4\pm0.13$	Man-plant	$1.6\pm0.17$	Under middle of leaf being yellow, tree crown decreasing
	South of Deng Kou Combating Desertification Bureau of Arboretum	July	7.5	$0.6\pm0.10$	$1.4\pm0.20$	Man-plant	$2.8\pm0.31$	Under middle of leaf being yellow, tree crown decreasing
Severe degeneration	Qing Sonbao, Zong He, Min Qin	Aug.	6.9	1.1 ± 0.11	$0.9\pm0.16$	Man-plant	$1.4\pm0.26$	Top of leaf being green most of leaf being yellow
Ç tanıt	East of Deng Kou Combating Desertification Bureau of Arboretum	Aug.	5.0	$0.5\pm0.09$	$0.8\pm0.12$	Man-plant	$1.2\pm0.29$	All of leaf being yellow
	West-north of Lin Zhe Combanting Station	July	7.0	$1.0\pm0.17$	$1.0\pm0.08$	Man-plant	$1.5\pm0.31$	All of leaf being yellow

## Table 5

Aeolian soil water content (%) (mean  $\pm$  SE) of the *H. ammodendron* natural community (No. 3) in June, July, and August of 1998 (n = 3).

Depth (cm)	June 15	July 10	August 20
0	$0.65\pm0.08$	$1.07\pm0.14$	$0.95\pm0.08$
20	$1.26 \pm 0.11$	$1.59\pm0.09$	$1.45\pm0.13$
40	$1.36 \pm 0.11$	$1.57 \pm 0.15$	$1.62 \pm 0.18$
60	$2.14\pm0.16$	$1.87 \pm 0.21$	$2.89 \pm 0.21$
80	$2.36\pm0.19$	$2.10\pm0.19$	$2.06\pm0.18$
100	$3.98 \pm 0.28$	$2.53 \pm 0.27$	$3.10\pm0.29$
150	3.86 ± 0.31	$3.86 \pm 0.29$	$3.08\pm0.16$
200	$4.21\pm0.35$	$4.01\pm0.34$	$4.36\pm0.37$

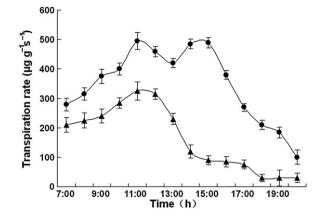


**Fig. 8.** Daily dynamics of the *E* of *H. ammodendron* in a natural community (No. 3) in June 15 (squares), July 10 (triangles), and August 20 (points) of 1998 (n = 5). Table 5 was the aeolian soil water content during the period of measurement.

# 3.6. E of H. ammodendron in different aeolian soil water contents

The aeolian soil water content increased with the increase of the soil depth in the natural stand (No. 3) in June, July, and August 1998 (Table 5). The daily *E* of *H. ammodendron* showed a single peak curve in different months under aeolian soil water content of over 2.0%. The daily *E* of *H. ammodendron* in July was significantly higher than that in June or in August (p < 0.05) (Fig. 8). The mean daily *E* in June, July, and August were 474.9, 539.2, and 472.9 µg g<sup>-1</sup> s<sup>-1</sup>, respectively.

The aeolian soil water content was higher in the No. 2 plantation than in the No. 1 from 20 cm to 200 cm soil depth (Table 6). The daily curve of *E* showed double peaks at a relatively higher aeolian soil water content (2.0%; No. 2). The first peak appeared at 12:00 with a value of 498.2  $\mu$ g g<sup>-1</sup> s<sup>-1</sup>, and the second peak appeared at 15:00 with a value of 486.5  $\mu$ g g<sup>-1</sup> s<sup>-1</sup>. Under less favorable aeolian soil water conditions (No. 1: aeolian soil water content < 2.0%), the *E* was similar to that of the No. 2 plantation in the morning. However, the *E* increased slightly later with the peak appearing at 12:00 with a value of 332.5  $\mu$ g g<sup>-1</sup> s<sup>-1</sup>, which was about 33% lower than that of the No. 2 plantation. The *E* of *H. ammodendron* in the No. 1 plantation then rapidly decreased, and its daily curve smoothened (Fig. 9). The daily mean value of the No. 1 plantation was only 177.2  $\mu$ g g<sup>-1</sup> s<sup>-1</sup>, which was about 50% lower than that of the No. 2 plantation.



**Fig. 9.** Daily dynamics of the *E* of Nos. 1 (triangles) and 2 (dots) plantations of *H. ammodendron* in July of 1999 (n = 5). Table 6 was the aeolian soil water content during the period of measurement.

# 4. Discussion

The *H. ammodendron* is a large shrub that grows in deserts with an arid climate. The shrub has formed a special water ecophysiological relationship with the environment in the long-term adaptation to the drought stress. A previous study showed that more than 90% of the feeder roots were in the 0 m to 0.9 m soil layer. The maximum depth of the *H. ammodendron* root was 3.32 m, which was far above the groundwater with a depth of 5.2 m (Xu et al., 2007). Stored aeolian soil water might be the main water source for the growth of *H. ammodendron* because of the lower groundwater table (deeper than 7.0 m) outside the Ulan Buh Desert.

The turning point of the aeolian soil water content for the plant growth was 2.0% in the Ulan Buh Desert. The aeolian soil water potential above this point declined by -0.18 MPa with every 1.0% decrease in the aeolian soil water content. When the aeolian soil water content is lower than this point, the slope of the linear relationship between the aeolian soil water content and the soil water potential is greater, the aeolian soil water content. Therefore, an aeolian water content of 2.0% appeared to be a critical value for the water traits of the aeolian soil in the Ulan Buh Desert.

The *H. ammodendron* had a very low  $\psi_x^{100}$  and  $\psi_x^0$ , which indicated the viscidity of the cell protoplasm in the assimilating shoot and the high bond ability of the bonding water (Hu and Wang, 1998; Zhang, 2000). Above an aeolian soil water content of 2.0%, the aeolian soil water potential was higher than -0.70 MPa. The osmotic potential of the assimilating shoot of the *H. ammodendron* was always lower than -2.82 MPa, which ensures that the water potential of the assimilating shoot is above the osmotic potential at zero turgor. When the aeolian soil water content was lower than 1.0%, the aeolian soil water potential of the assimilating shoot of *H. ammodendron* could not be restrained despite the osmotic potential decrease at lower than -3.41 MPa.

The daily curve of the water potential of the assimilating shoot declined with the decrease of the aeolian soil water content. The *H. ammodendron* would benefit from acquiring water from soil. The relationship between the predawn water potential and the midday or

Table 6Aeolian soil water content (%) in 2 different plantations of *H. anmodendron* in 1999 (n = 3).

	•		, ,					
Depth (cm)	0	20	40	60	80	100	150	200
8- to 10-year plantation (No. 1)	$0.66\pm0.07$	$0.48\pm0.06$	$0.65\pm0.08$	$1.09\pm0.09$	$1.22\pm0.09$	$1.63\pm0.15$	$1.70\pm0.11$	$1.63\pm0.14$
8- to 10-year plantation (No. 2)	$0.44 \pm 0.08$	$0.66 \pm 0.06$	$0.79 \pm 0.07$	$1.36 \pm 0.14$	$1.56 \pm 0.13$	$2.16 \pm 0.19$	$3.02 \pm 0.25$	$2.91 \pm 0.17$

evening water potential of the *H. ammodendron* was linear. The predawn water potential declined more than midday water potential when the aeolian soil water content decreased. The total daily curve of the water potential smoothened. The variation of the water potential of *H. ammodendron* accelerated when the aeolian soil water content was lower than 2.0%. In the south edge of the Gurbantonggut Desert of Xinjiang, *H. ammodendron* used the rain-derived upper soil water for survival and responded to the rain pulse events in terms of leaf water potential and transpiration. The plant was able to maintain normal photosynthesis within a wide range of soil water status (Xu and Li, 2006). In the absence of precipitation, both the predawn and midday water potential of *H. ammodendron* continually decreased over time in response to the lack of water (Xu et al., 2007).

The predawn water potential of the assimilating shoot of H. ammodendron was -2.82 MPa when the aeolian soil water content was 2.0%. The potential was the boundary from the linear decrease to the curved decrease and was similar to the critical value (Guo and Tian, 1992). The ecological importance was analyzed as follows: water potential of the assimilating shoot of the *H. ammodendron* was slightly affected by the variation of the aeolian soil water content when above 2.0%. The water potential of the assimilating shoot recovered to above the zero point of the turgor after one night. The growth of the H. ammodendron would not be affected by water stress. However, rapid and obvious decline in the water potential of the assimilating shoot occurred as evidenced by the slight decrease of the soil water content and severe water stress when the aeolian soil water content was lower than 2.0%. The minimum value of the aeolian soil water content was 1.0% for the growth of the H. ammodendron. The corresponding soil water potential was -2.82 MPa. The water potential of the assimilating shoot was -3.50 MPa, which was lower than  $\psi_x^0$  (-3.41 MPa), which means that the turgor could not recover. A similar result was reported in other areas. In the Gurbantonggut Desert, the seasonal pattern of the predawn water potential of H. ammodendron was closely related to the soil moisture in the upper layer at a depth of 0 m to 0.2 m and 0.6 m to 0.8 m, which was periodically recharged by rain events and acutely responded to rainfall above 5 mm (Xu et al., 2011). A recent study indicated that the critical value of the water potential of H. ammodendron was also affected by soil texture. For example, H. ammodendron defoliated when the predawn leaf water potential dropped below -3.00 MPa in sandy soil. Defoliation also occurred when the predawn leaf water potential dropped below -3.75 MPa in heavy-textured soil (Zou et al., 2010).

*H. ammodendron* normally grows under favorable aeolian soil water conditions (soil water content > 2.0%) with an "arch" shape *E* daily curve. When the aeolian soil water content declined below 2.0%, soil water became a main factor that affected the *E* of *H. ammodendron*. The cause for the double peaks, the disappearance of the second peak, and the plateaued total curve resulted from water stress. The daily mean *E* of *H. ammodendron* decreased by more than 80% to save water. After the relative water deficit decreased to lower than 1.0%, the cell turgor disappeared, and the osmotic potential became lower than -3.41 MPa. However, the assimilating shoot of *H. ammodendron* did not wither because of the succulence of the shoot. In the absence of precipitation, the *E* of *H. ammodendron* continually decreased over time in response to the lack of water (Xu et al., 2007).

The water ecophysiological traits of *H. ammodendron* may have benefitted from its adaptation to extreme desert conditions. For example, *H. ammodendron* had a lower water loss, which is suitable for desert conditions because of the low *E* and low water potential, compared with other plants in the Heihe basin of Northwest China such as *Calligonum mongolicum*, *Elaeagnus angustifolia*, and *Populus hosiensis* (Gong et al., 2006). Given the actual survey results, we have reason to believe that the P–V water parameter of *H. ammodendron* can be considered as the water threshold. An "economic water threshold" (aeolian soil moisture threshold for normal growth) of the *H. ammodendron* could be around 2.0% for a normal dry matter accumulation in the aeolian soil. The predawn water potential of the assimilating shoot can recover to above the zero turgor only when the aeolian soil water content is higher than the "economic water threshold." An aeolian soil water content of about 1.0% is called the "survival water threshold" (aeolian soil moisture threshold for survival) of the *H. ammodendron* for normal growth. When the aeolian soil water content is lower than the "survival water threshold," the predawn water potential of the assimilating shoot cannot recover to the zero turgor.

# Acknowledgments

This study was supported by the National Basic Research Program of China ('973' Project, Project No. 2013CB429901) and by the National Natural Science Foundation of China (Grant Nos. 31170667).

# References

- Gao, S., Su, P.X., Yan, Q.D., Ding, S.S., 2010. Canopy and leaf gas exchange of *Haloxylon* ammodendron under different soil moisture regimes. Science China. Life Sciences 53, 718–728.
- Gong, J.R., Zhao, A.F., Huang, Y.M., Zhang, X.S., Zhang, C.L., 2006. Water relations, gas exchange, photochemical efficiency, and peroxidative stress of four plant species in the Heihe drainage basin of northern China. Photosynthetica 44, 355–364.
- Guo, L., Tian, Y., 1992. Relationship between leaf water potential of eight broadleaved and coniferous young trees in early morning and soil moisture content and drought resistance of these trees. Chinese Journal of Ecology 11, 4–7.
- Han, W., Xu, X.W., Li, L., Lei, J.Q., Li, S.Y., 2010. Chlorophyll a fluorescence responses of *Haloxylon ammodendron* seedlings subjected to progressive saline stress in the Tarim desert highway ecological shelterbelt. Photosynthetica 48, 635–640.
- Hu, X.S., Wang, S.J., 1998. A review of studies on water stress and drought tolerance in tree species. Scientia Silvae Sinica 34, 77–89.
- Li, C., Li, Y., Ma, J., 2011. Spatial heterogeneity of soil chemical properties at fine scales induced by *Haloxylon ammodendron* (Chenopodiaceae) plants in a sandy desert. Ecological Research 26, 385–394.
- Liu, J.L., Wang, Y.G., Yang, X.H., Wang, B.F., 2011. Genetic variation in seed and seedling traits of six *Haloxylon ammodendron* shrub provenances in desert areas of China. Agroforestry Systems 81, 135–146.
- Shan, L.S., Zhang, X.M., Wang, Y.K., Wang, H., Yan, H.N., Wei, J., Xu, H., 2008. Influence of moisture on the growth and biomass allocation in *Haloxylon ammodendron* and *Tamarix ramosissima* seedlings in the shelterbelt along the Tarim Desert Highway, Xinjiang, China. Chinese Science Bulletin 53 (Supp. II), 93–101.
- Su, P., Cheng, G., Yan, Q., Liu, X., 2007. Photosynthetic regulation of C4 desert plant Haloxylon ammodendron under drought stress. Plant Growth Regulation 51, 139–147.
- Tyree, M.T., Hammel, H.T., 1972. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. Journal of Experimental Botany 23, 267–282.
- Wei, J., Zhang, X.M., Yang, H.L., Liang, S.M., 2007. Seedling growth dynamic of *Haloxylon ammodendron* and its adaptation strategy to habitat condition in hinterland of desert. Science China Earth Sciences 50 (Supp. I), 107–114.
- Wu, Z.Y., 1979. Flora Repubulicae Popularis Sinicae. Angiospermae, Dicotyledoneae, Chenopodiaceae, Amaranthaceae, Science Press, vol. 25 (2) (Beijing).
- Xu, H., Li, Y., 2006. Water-use strategy of three central Asian desert shrubs and their responses to rain pulse events. Plant and Soil 285, 5–17.
- Xu, H., Li, Y., Xu, G., Zou, T., 2007. Ecophysiological response and morphological adjustment of two Central Asian desert shrubs towards variation in summer precipitation. Plant, Cell and Environment 30, 399–409.
- Xu, H., Zhang, X.M., Yan, H.L., Liang, S.M., Shan, L.S., 2008. Plant water status of the shelterbelt along the Tarim Desert Highway. Chinese Science Bulletin 53 (Supp. II), 146–155.
- Xu, G., Li, Y., Xu, H., 2011. Seasonal variation in plant hydraulic traits of two co-occurring desert shrubs, *Tamarix ramosissima* and *Haloxylon ammodendron*, with different rooting patterns. Ecological Research 26, 1071–1080.
- Zhang, G.S., 2000. Research progress on trees and shrub drought-resistance and woodland water activity in arid and semi-arid region. Journal of Design Research 20, 363–368.
- Zhou, Z.Y., Li, F.R., Chen, S.K., Zhang, H.R., Li, G., 2011. Dynamics of vegetation and soil carbon and nitrogen accumulation over 26 years under controlled grazing in a desert shrubland. Plant and Soil 341, 257–268.
- Zou, T., Li, Y., Xu, G.Q., 2010. Responses to precipitation treatment for Haloxylon ammodendron growing on contrasting textured soils. Ecological Research 25, 185–194.