

Root distribution of three dominant desert shrubs and their water uptake dynamics

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Abstract

Aims

Root architecture is a crucial determinant in the water use of desert shrubs. However, lack of integrated research on the root functional type and water uptake dynamic hinders our current understanding of the water-use strategies of desert species.

Methods

A field experiment was conducted to investigate the root functional type of three dominant desert species, *Haloxylon ammodendron*, *Nitraria tangutorum* and *Calligonum mongolicum*, and the dynamics of their root water uptake. The stem sap flow and microclimate were monitored, and the intact root systems of these shrubs were excavated in their native habitats on the oasis-desert ecotone of northwestern China during the summer of 2014.

Important Findings

Based on root functional type, *H. ammodendron* is phreatophytic, while *N. tangutorum* and *C. mongolicum* are non-phreatophytic species, which means *H. ammodendron* can utilize multiple potential water sources, *N. tangutorum* and *C. mongolicum* mainly utilize shallow and middle soil water. The average root

water uptake rates (RWU) of *H. ammodendron*, *N. tangutorum* and *C. mongolicum* were 0.56 (± 0.12), 1.18 (± 0.19) and 1.31 (± 0.30) kg m⁻² h⁻¹, respectively, during the experimental period; the contributions of night-time RWU to total water uptake amount for the corresponding species were 12.7, 2.9 and 10.6%, respectively. The diurnal and seasonal dynamics of RWU in the three species were significantly different ($P < 0.05$), and closely related to environmental variables, especially to photosynthetically active radiation and vapor pressure deficit. Our results suggested that the three species have distinct water-use patterns in combination with the patterns of root distribution, which may alleviate water competition during long-term water shortages. *H. ammodendron* appears to be more drought tolerant than the other species due to its use of multiple water sources and stable water uptake rates during growing season.

Keywords: root architecture, stem sap flow, water-use strategy, arid region, desert shrub

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INTRODUCTION

Roots perform a variety of functions critical to the survival of all plants (Jackson *et al.* 1996). One key function is their ability to transport water and other substances from the soil to the plant to the atmosphere along a continuum of increasingly negative water potential (Chahine 1992; Feddes *et al.* 2001; Jackson *et al.* 2000; Jing *et al.* 2014). Water uptake by roots is a complex process, determined by the interaction of

physical and physiological processes in the soil–root system (Green and Clothier 1999; Green *et al.* 2003). The effect of root distribution on root water uptake has been well documented by many researches (Ellsworth and Stenberg 2014; Ferchaud *et al.* 2015; Grimaldi *et al.* 2015; Moroke *et al.* 2005; Wu *et al.* 1999; Yu *et al.* 2007). For desert plants, the root architecture is particularly important for plant growth and closely relate with plant–water relations (Chimner and Cooper 2004; Poot and Lambers 2008).

It is generally agreed that desert shrubs have evolved special morphological and physiological characteristics to adapt to extreme drought environments (Chimner and Cooper 2004; Dawson and Pate 1996; Lawlor and Cornic 2002). Because of the high evaporative demand during the growing season and rapid depletion of water in the surface soil after rainfall, desert species need to extract water by extending their root systems, thus increasing their drought tolerance (Carter and White 2009). Therefore, the phenotype of the root system (one of the most important morphological features) is a crucial determinant for plant survival in arid ecosystems (Berndtsson et al. 1996; Ehleringer 1984; McVicar et al. 2007).

Haloxylon ammodendron, *Nitraria tangutorum* and *Calligonum mongolicum* are mainly distributed along the edge of oasis in the arid region, northwestern China (Ji et al. 2006; Kang et al. 2007). All species are of great ecological and economic importance and are crucially important in stabilizing sand dunes (Cao et al. 2011; Feike et al. 2014). Previous studies have focused on leaf-scale transpiration and photosynthesis (Pyankov 1999; Qiu et al. 2015; Su et al. 2004, 2007; Yan et al. 2010) and the physiological response of their leaves to rainfall (Dai et al. 2014; Li 2008; Wu et al. 2014; Xu and Li 2006; Xu et al. 2007; Zou et al. 2010). The rooting patterns of the three shrubs have also been investigated to elucidate the water-use strategies during drought periods (Song et al. 2011; Xu and Li 2008; Xu et al. 2011; Zou et al. 2010). All these researches provide valuable information for us to understand the eco-physiological response and morphological adjustment of desert plants towards extreme drought environment.

However, the researches described above only focused on one or two species. Though the differences of water-use strategy of desert shrubs were compared, a complete investigation about the water-use pattern of *H. ammodendron*, *N. tangutorum* and *C. mongolicum* co-occurring in the oasis-desert ecotone is still lacking. Particularly, the relationship between root functional type and water uptake dynamics for these shrubs remain unexplored. Therefore, integrated research on root distributions, water uptake patterns and their responses to environmental variables need further investigation to understand the water use of these species.

In this study, our main objectives are: (1) to investigate the root distribution architecture of the three native dominant species in the arid region of northwestern China, (2) to analyze the characteristics of water uptake dynamics during the growing season and their response to environmental variables and (3) to examine differences of water-use strategy among the three species. Due to these desert species co-dominant in the studying area, we hypothesize that they would develop different root architecture to alleviate water resource competition, thus affect their course of water uptake dynamics and response to environmental conditions. This study will provide a better understanding of the function of root architecture related to water resources and afforestation management, which play unique roles in protecting oases from desertification.

MATERIAL AND METHODS

Field site and study species

We conducted our experiment from June to August 2014 near the Linze Inland Basin Research Station, Chinese Academy of Sciences, located in the middle of the Hexi Corridor, northwestern China (39°22'07" N, 100°08'48" E, 1386 m a.s.l.) (Fig. 1). The environment is characterized by a typical continental arid temperate climate, with dry and hot summers and cold winters. Annual mean precipitation is about 125 mm, with more than 80% occurring from June to September. Annual mean temperature is about 8.9°C, with the lowest temperature of −26.2°C occurring in January and the highest temperature of 38.6°C occurring in July. Soil at the site is loamy sand (sand 73.5%, silt 22.5% and clay 1.4%) (USDA texture class) with little organic matter and few mineral nutrients. The average bulk density, field capacity and wilting point are 1.55 g cm^{−3}, 0.28 and 0.05 cm³ cm^{−3}, respectively. The average groundwater table in the study area is 4.2 m, and ranged from 4.15 to 4.29 m during the experimental period.

Haloxylon ammodendron, *N. tangutorum* and *C. mongolicum* are our target species because they are dominant native species and critical for stabilizing sand dunes. We selected three sampled plants for each species to conduct our tests. The estimated leaf area index, on a crown projected area basis, was determined using a destructive method at the end of the study. Selected characteristics for each sampled plant are listed in Table 1.

Sap flow measurements

Because the roots of these shrubs were too thin to install the gauges, the root water uptake was represented by stem sap flow. Root water uptake (RWU) rate was presented as water use (kg) per unit root surface area (m²) per unit time (h). Commercially available, constant power stem sap flow gauges (Flow32 meters, Dynamax Inc., Houston, TX, USA) based on the heat balance method (Baker and Bavel 1987; Sakuratani 1981; Steinberg et al. 1989) were used. We installed gauges on the base of the stems (three individual trees for each species)

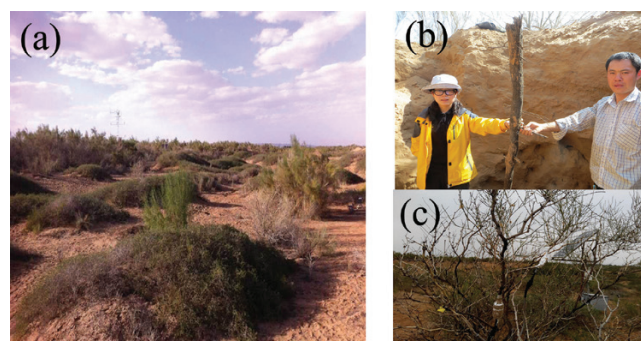


Figure 1: photographs of the study area (a), sap flow measurement (b) and root excavation (c).

following the manufacturer’s instruction (Dynamax 2009) and their detailed information was listed in the Table 2.

To ensure good thermal contact between the stem surface and thermocouples, and to prevent sensor corrosion and normal stem respiration, we prepared the stems by minimal sanding and coated them with a layer of silicone-based dielectric grease. The gauges were removed and reinstalled on different stems after about the 2-week measuring period to minimize the likelihood of stem damage caused by construction, silicone grease and sensor heating (Grime and Sinclair 1999). Raw signal data from the gauges was recorded at 10-s interval and stored as 30-min averaged by a Campbell CR1000 data logger (Cambell Scientific Inc., Logan, UT, USA).

Environmental measurements

We constructed a standard automatic weather station at the top of a 4-m high scaffold tower to measure photosynthetically active radiation (PAR) (Li-190SB, Li-Cor Inc., Lincoln, NE, USA), air temperature (HMP155A, Vaisala, Helsinki, Finland), relative humidity (HMP155A, Vaisala, Helsinki, Finland), rainfall (TE525, Texas Electronics Inc., Dallas, TX) and wind speed and direction (1405-PK-052, Gill Instruments Ltd., Lymington, UK) at the site. We recorded measurements as 30-min averages using a CR1000 data logger, and calculated vapor pressure deficit (VPD) (kPa) using temperature and humidity measurement. We measured volumetric soil water content with the Time Domain Reflectometers (TDR,

CS616, Campbell Scientific Inc., Logan, UT, USA) using 12 probes at depths of 10, 20, 40, 60, 80 and 120 cm and recording the data with a CR1000 data logger at 30-min intervals.

Root excavation

After the stem sap flow measurement, we excavated the intact root systems of the sampled plants to determine their root distribution (Fig. 1). We dug a ring ditch around each plant, basing the diameter of the excavation on earlier preliminary investigations of plant species in this region and an estimate of the horizontal root extension. We manually removed the large soil cylinder surrounding the main root at 10 cm intervals to progressively expose the roots layer by layer. Roots with diameters less than 0.2 mm were not recorded, as they broke away as the soil was manually removed. Roots with decayed surfaces were also not recorded, as they had lost the ability to absorb water and nutrients. The characteristics of the root system that we measured included root length density (RLD, cm cm⁻³), root surface area density (RAD, cm² cm⁻³) and root dry biomass (RDB, g). Additionally, we divided roots into three diameter size classes: coarse roots (>3 mm), medium-size roots (1–2 mm) and fine roots (<1 mm).

Data analysis

Data analysis and charting was processed using the statistics software Origin 9.0 (OriginLab Corp., Northampton, MA, USA). We used one-way analysis of variance (ANOVA) to test for differences among data measured for three species.

Table 1: characteristics of the sampled plants

Species	Height (m)	Canopy area (m ²)	Diameter of excavation ditch (m)	Depth of excavation (m)	Leaf area index	Root/shoot ratio	Code
<i>H. ammodendron</i>	1.12	1.04	1.60	2.50	0.64	0.90	H1
	2.10	2.01	3.00	2.60	0.48	0.97	H2
	3.06	5.30	4.00	4.20	0.22	1.35	H3
<i>N. tangutorum</i>	0.48	0.95	1.50	0.70	0.6	0.40	N1
	0.54	2.13	1.80	0.90	0.58	0.47	N2
	0.66	8.50	3.40	1.60	0.32	0.64	N3
<i>C. mongolicum</i>	0.96	1.05	1.20	0.70	0.73	0.86	C1
	1.20	1.13	1.40	0.90	0.62	0.87	C2
	1.36	2.3	1.70	1.20	0.55	1.05	C3

Table 2: detailed information about the installed gauges used to measure the stem sap flow

Species	Type of gauges	Stem diameter (mm)	Measured tree	Code	Species	Type of gauges	Stem diameter (mm)	Measured tree	Code
<i>H. ammodendron</i>	SGA5	5.60	H1	G1	<i>N. tangutorum</i>	SGA3	3.40	N1	G7
	SGA13	13.05	H1	G2		SGA3	3.20	N2	G8
	SGA13	14.55	H2	G3		SGA3	3.60	N3	G9
	SGB19	20.35	H2	G4	<i>C. mongolicum</i>	SGA5	5.50	C1	G10
	SGA25	24.80	H3	G5		SGA9	1.00	C2	G11
	SGA25	26.35	H3	G6		SGA13	13.70	C3	G12

The z-score method was applied to normalize the data of RLD, RAD and RDB for each sampled tree as follows

$$x^* = \frac{x - \mu}{\sigma} \quad (1)$$

where X^* is the normalized data, X is the measured data, μ is the mean of the sample data and σ is the standard deviation of the sample data.

We applied the global model (Gale and Grigal 1987; Jackson et al. 1996) to describe the relationship between root distribution and soil depth

$$Y_z = 1 - \beta^Z \quad (2)$$

where Z is soil depth measured from the surface (cm), Y_z is the cumulative root fraction at soil depth Z and β is a dimensionless root extinction parameter fitted using the least square method. The following equations were used to calculate the value Y_z

$$Y_z = \sum_{i=10}^z P_{Z(i)} \quad (3)$$

$$P_z = \frac{RLD_z}{RLD_{total}} \quad (4)$$

where P_z is the relative proportion of root length density (RLD) at the soil depth Z , RLD_z is the root length density at soil depth Z , RLD_{total} is the sum of root length density at every soil depth.

In our study, the dependency of root water uptake on the environmental conditions was described by Stöhr and Lösch (2004)

$$W = W_{max} * \frac{f_x}{W_{max}} * \dots * \frac{f_g}{W_{max}} \quad (5)$$

where W is the estimated RWU ($\text{kg m}^{-2} \text{h}^{-1}$), W_{max} is maximum of the measured RWU rate, x, \dots , and g are the environmental drivers such as PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$), temperature ($^{\circ}\text{C}$), VPD (kPa), etc. The subfunction f was fitted based on the relationship between root water uptake and instantaneous environmental variables.

In order to estimate the RWU rate, the data for each species were divided into two groups (one contained data in the order of 1, 3, 5... and the other 2, 4, 6..., respectively). The first group was used to train the model, and the second group was used to test the model.

RESULTS

Environmental conditions

During the experimental period, the maximum of monthly average VPD (1.9 kPa) and PAR ($570.7 \mu\text{mol s}^{-1} \text{m}^{-2}$) occurred in July (Fig. 2a), reflecting the high atmospheric evaporative demand in this month. A total rainfall was 113.4 mm, with 77.3% of the rainfall occurring in summer (Fig. 2b). The soil moisture in the study area responded to rainfall till up to 80 cm layer, under which soil water content generally maintain stable during the experimental period.

Root distribution

The vertical distributions of RLD, RAD and RDB for three species are presented in Fig. 3.

For *H. ammodendron*, only a few active absorbing roots were found in the upper 0–10 cm of the soil profile and more than 68% of roots were distributed from 10 to 100 cm. The highest RLD, RAD and RDB for sampled plants occurred at depth of 20–40 cm, and decreased with depth (Fig. 3a). The tap root of *H. ammodendron* can extended to 420 cm depth. Therefore,

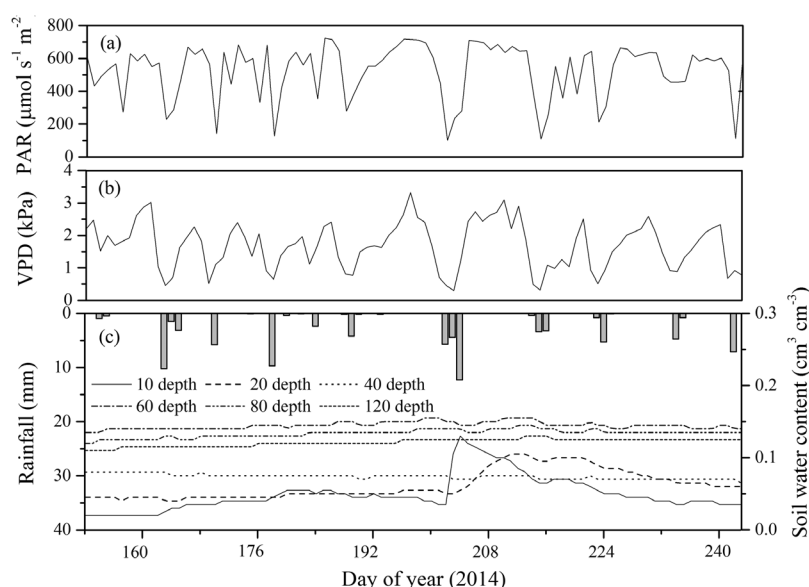


Figure 2: variation of daily PAR (a), VPD (b) and rainfall (columns) and soil volumetric moisture content at six different depths (c).

shrubs of this species were able to effectively utilize deep soil water or shallow groundwater.

For *N. tangutorum*, about 50% of roots occurred at the depth of 0–30 cm and then decreased rapidly below 30 cm layer. The tap root of *N. tangutorum* extended to 160 cm depth, far above the averaged 4.2 m shallow groundwater table (Fig. 3b). The root structure characteristics indicated that this species mainly used shallow soil water replenished by rainfall and middle soil water recharged by capillary rise of ground water.

For *C. mongolicum*, the highest RLD, RAD and RDB occurred in the surface soil with more than 63% of roots distributed at

layer of 0–20 cm, decreasing below 20 cm (Fig. 3c). The tap root of *C. mongolicum* can extended to 120 cm depth, suggesting that this species is mainly dependent on shallow soil water or middle soil water.

We also observed that the distribution of RLD, RAD and RDB were relatively consistent for each sampled plant (Fig. 3).

Comparison with global Jackson model

The computed root extinction coefficient values (β) for three species were presented in Fig. 4. It can be seen that the computed β value for *H. ammodendron* was higher than *N. tangutorum* and *C. mongolicum*.

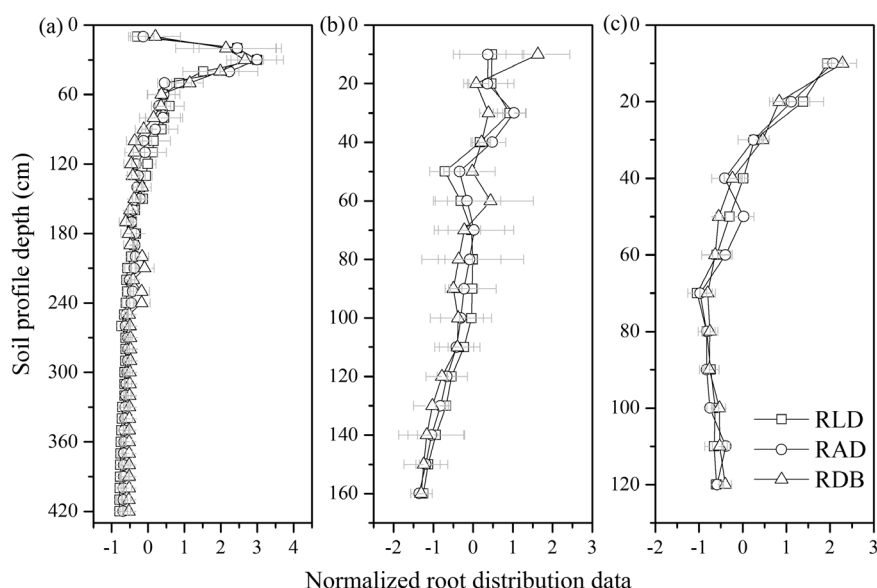


Figure 3: vertical distribution of RLD, RAD and RDB normalized using the z-score method for *H. ammodendron* (a), *N. tangutorum* (b) and *C. mongolicum* (c).

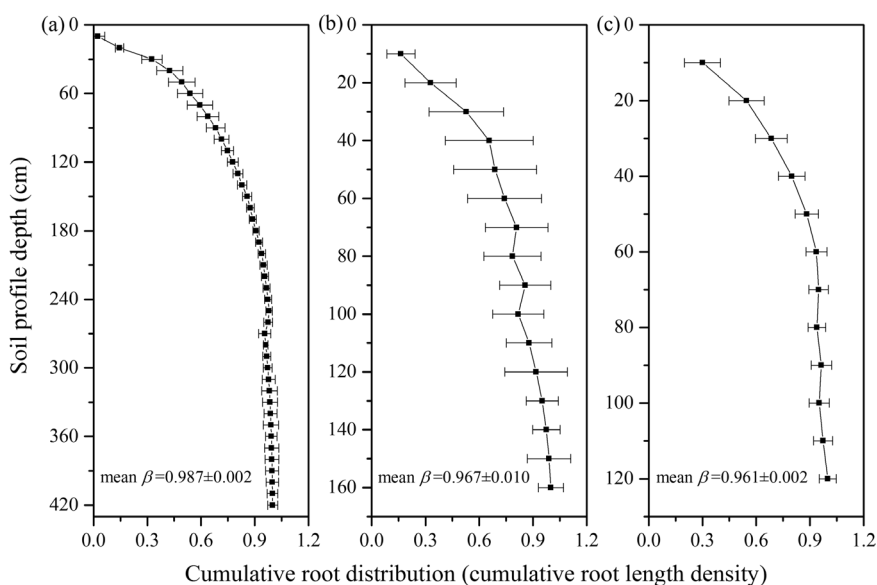


Figure 4: cumulative root distribution (RLD) plotted against the soil depth for *H. ammodendron* (a), *N. tangutorum* (b) and *C. mongolicum* (c).

Comparison with natural vegetation ecosystems based on the Jackson *et al.* (1996) model showed that the computed root extinction coefficient value (β) for *H. ammodendron* (mean $\beta = 0.987 \pm 0.002$) was higher than that of desert biome ($\beta = 0.975$). As Jackson *et al.* (1996) model only measured nine root distributions to at least 2 m, for deep-rooted *H. ammodendron*, which could extend its tap root to shallow groundwater table, the β were expected to be higher. Values for *N. tangutorum* (mean $\beta = 0.967 \pm 0.010$) and *C. mongolicum* (mean $\beta = 0.961 \pm 0.002$) were lower than that of desert biome, but closed to that of sclerophyllous shrubs ($\beta = 0.964$).

Distribution of different-size root diameter

Haloxylon ammodendron had a significantly higher proportion of fine root diameter compared to *C. mongolicum* and *N. tangutorum* (Table 3). We also observed that the vertical distribution of proportion of fine root diameter for *N. tangutorum* and *C. mongolicum* was in accordance with their vertical distribution of RLD, RAD and RDB (Figs 3 and 5). That is, their proportion of fine root diameter was highest in surface soil layer and decreased with depth, while this was not significant in *H. ammodendron*. So, we presumed that *H. ammodendron* could utilize more deep soil water because of the relative high proportion of fine root

diameter in deep soil, though the highest RLD, RAD and RDB for this species occurred mainly at the layer of 20–40 cm.

Diurnal and seasonal root water uptake

We observed significant differences ($P < 0.05$) among the RWU rates of the three species during the summer of 2014 (Fig. 6). The average RWU of *H. ammodendron*, *N. tangutorum* and *C. mongolicum* were $0.56 (\pm 0.12)$, $1.18 (\pm 0.19)$ and $1.31 (\pm 0.30)$ $\text{kg m}^{-2} \text{h}^{-1}$, respectively. The RWU of *H. ammodendron* ranged from 0.00 to $2.18 (\pm 0.44)$ $\text{kg m}^{-2} \text{h}^{-1}$, RWU of *N. tangutorum* ranged from 0 to $5.22 (\pm 1.32)$ $\text{kg m}^{-2} \text{h}^{-1}$, and RWU of *C. mongolicum* ranged from 0.00 to $5.78 (\pm 1.12)$ $\text{kg m}^{-2} \text{h}^{-1}$.

Two consecutive clear days in each month were selected to illustrate the changing diurnal trend. RWU of three species began with sunrise and increased sharply during the first several hours of sunlight, increasing to midday (06:00–12:00 hours) as the PAR and air temperature increased. It reached a maximum at about 12:00–13:00 hours, and then decreased after about 16:00–19:00 hours before sunset (Fig. 6a–c). In addition, as shown in Fig. 6a–c, in the main growing season, there was still relative low RWU at night-time (20:00–06:00) for each species, and it was more significant in *H. ammodendron* compared to other two species. The diurnal variation of RWU showed a multimodal patterns for three species during the different months. *H. ammodendron* and *N. tangutorum* had significant ‘noon depression’, while it was not obvious in *C. mongolicum*. It was possible that the stomata of *H. ammodendron* and *N. tangutorum* are closed to some extent and RWU therefore was inhibited.

Furthermore, the daily RWU pattern differed seasonally, and the peak value occurred in July for *H. ammodendron* and *C. mongolicum*, and in August for *N. tangutorum* (Fig. 6d), indicating that the extremely high atmosphere evaporative demand would impose water stress on *N. tangutorum* in July to a certain extent, a species using the C_3 photosynthetic

Table 3: frequency distribution of different-size root diameter for three species

	<i>H. ammodendron</i>	<i>N. tangutorum</i>	<i>C. mongolicum</i>
Coarse roots (>3 mm)	0.08 ± 0.03	0.37 ± 0.07	0.23 ± 0.04
Medium-size roots (1–3 mm)	0.42 ± 0.05	0.37 ± 0.04	0.36 ± 0.02
Fine roots (<1 mm)	0.50 ± 0.08	0.26 ± 0.06	0.42 ± 0.07

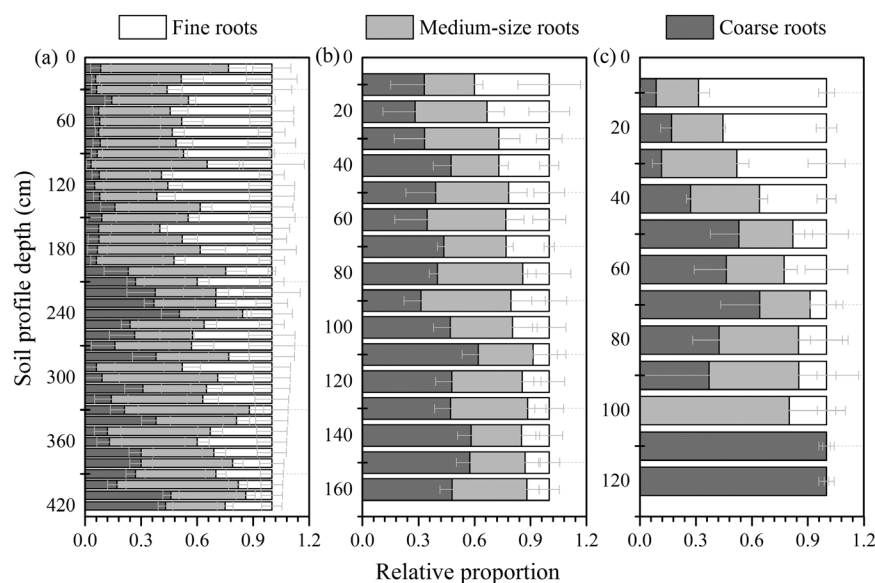


Figure 5: vertical distribution of relative proportion of different-size root classes for *H. ammodendron* (a), *N. tangutorum* (b) and *C. mongolicum* (c).

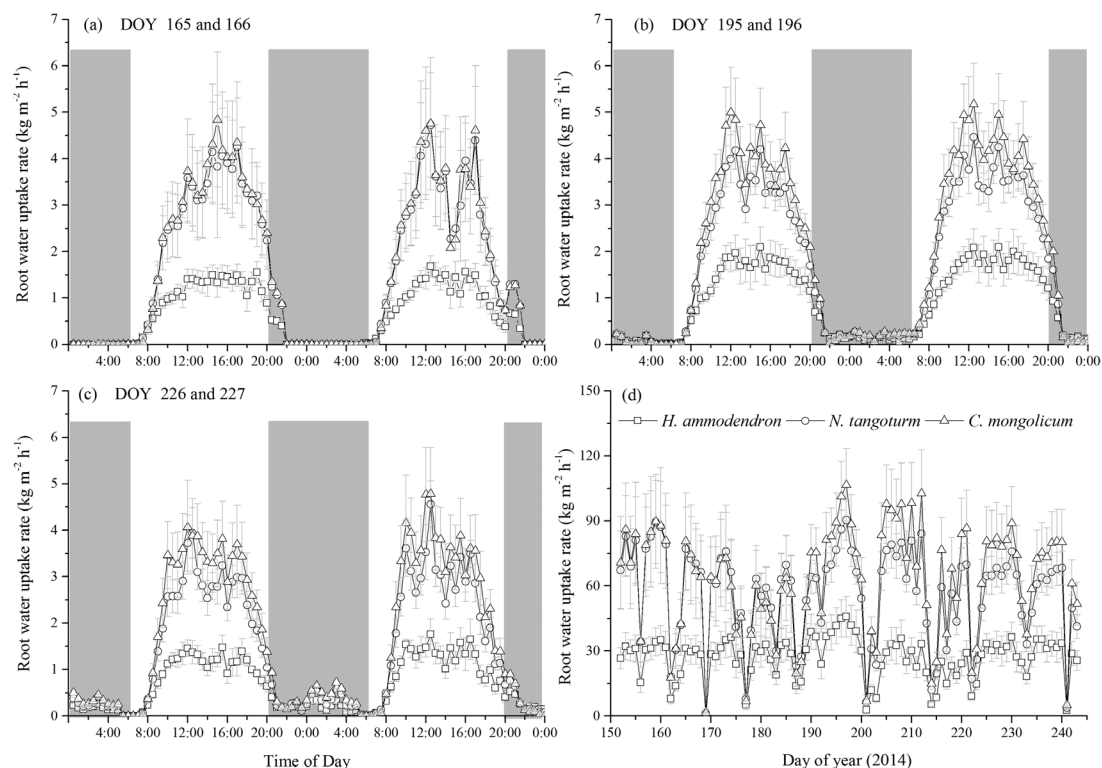


Figure 6: dynamics of the RWU rates for *H. ammodendron*, *N. tangutorum*, and *C. mongolicum* in June (a), July (b), August (c) and growing season (d) (the shaded area is night time).

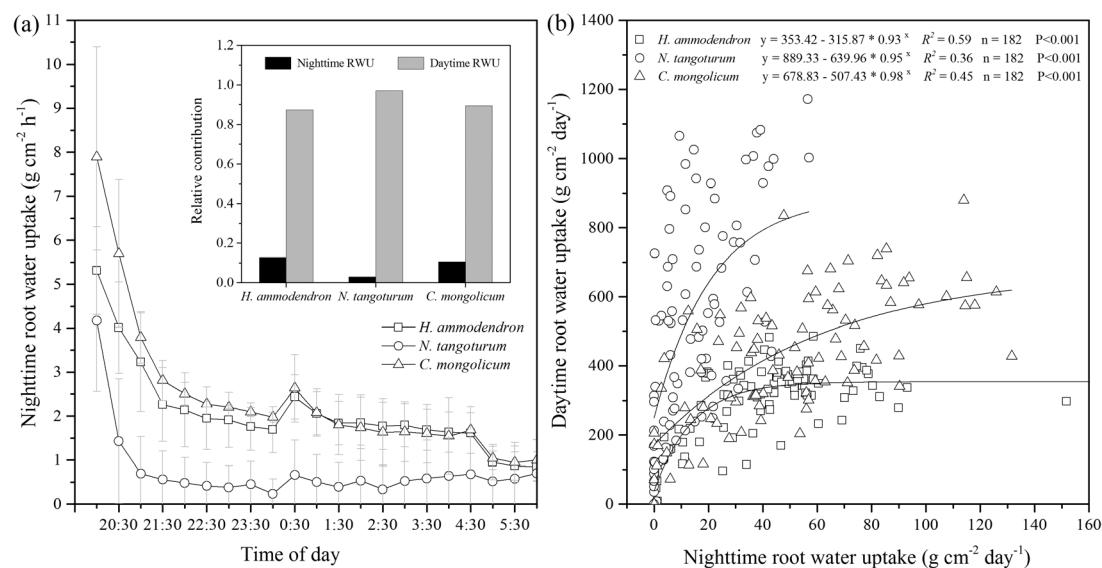


Figure 7: dynamics of night-time root water uptake for three species (a) and relationship between night-time RWU rates and daytime RWU rates (b).

pathway, than on *H. ammodendron* and *C. mongolicum*, species using the C_4 photosynthetic pathway.

Haloxylon ammodendron maintained more stable RWU during the experimental period than other two species (Fig. 6d). The daily RWU of *H. ammodendron* ranged from $0.55 (\pm 0.12)$ to $45.77 (\pm 3.40)$ $\text{kg m}^{-2} \text{day}^{-1}$, daily RWU of *N. tangutorum* ranged from $1.2 (\pm 0.09)$ to $90.36 (\pm 9.21)$ $\text{kg m}^{-2} \text{day}^{-1}$, and

daily RWU of *C. mongolicum* ranged from $1.41 (\pm 0.05)$ to $106.58 (\pm 6.74)$ $\text{kg m}^{-2} \text{h}^{-1}$, respectively.

Night-time root water uptake

In this article, the night-time RWU was determined between 20:00 to 06:00 hours when solar radiation was less than 5.0 W m^{-2} (Daley and Phillips 2006). As shown in Figs 6 and 7a,

night-time RWU fluctuated significantly for three species and relatively higher before midnight, after that, it approached a steady state. During the studying period, the contribution of night-time RWU to total water uptake amount for *H. ammodendron*, *N. tangutorum* and *C. mongolicum* was 12.7, 2.9 and 10.6 %, respectively. The night-time RWU positively responded to the daytime RWU.

Response of root water uptake to environmental variables

The RWU in three species varied in response to environmental conditions. In Fig. 8, the first and forth axes can explain most of the variation. Nearly all the environmental variables were significant for RWU of three species (Table 4), indicated a strong correlation between RWU and environmental conditions. The redundancy analysis (RDA) and Kendall's tau values (R) suggested that PAR and VPD had the strongest influence on whole time RWU, $R = 0.90$, 0.82 , 0.88 and 0.64 , 0.58 , 0.65 , respectively. Soil moisture (0–20 cm depth) had the least effect on RWU. Night-time RWU in three species were significantly correlated with air temperature and VPD (Table 4).

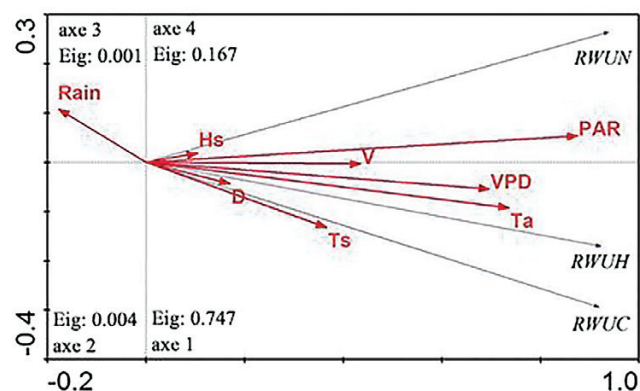


Figure 8: RDA for the relationship between root water uptake and the meteorological variables. RWUH, RWU rates in *H. ammodendron*; RWUN, RWU rates in *N. tangutorum*; RWUC, RWU rates in *C. mongolicum*; Ta, air temperature ($^{\circ}\text{C}$); rain, rain fall (mm); Ts, soil temperature ($^{\circ}\text{C}$); Hs, soil moisture ($\text{cm}^3 \text{ cm}^{-3}$); V, wind velocity (m s^{-1}); D, wind direction ($^{\circ}$).

We analyzed the relationship between the hourly RWU of three species and both PAR and VPD (Fig. 9). The result indicated that high PAR and VPD values could lead to high RWU. The RWU changed greatly when PAR and VPD increased. Their relationship can be explained well by a two-dimensional response function, the R^2 of the regression coefficient between measured RWU values and estimated values were 0.78, 0.62 and 0.75, respectively for *H. ammodendron*, *N. tangutorum* and *C. mongolicum* (Fig. 9). As shown in Fig. 9, the minimum threshold of VPD driving force can be seen to be around 1.5 kPa and the optimal PAR was about $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

DISCUSSION

As a result of low precipitation and high atmospheric evaporative demand, the three dominant desert shrubs in our study—*H. ammodendron*, *N. tangutorum* and *C. mongolicum*—are likely subjected to long-duration water shortages during the growing season. As a result, these species have developed specific root architecture for surviving and acclimating in the severely water-limited environment.

As a phreatophyte, *H. ammodendron* is able to sustain itself through frequent water shortages occurring in the upper soil layer and maintain a stable RWU rate (Fig. 6). The vertical root distribution and component of root diameter classes revealed that this species can utilize multiple water sources (Figs 3 and 5, Table 3), which is consistent with the findings of Xu and Li (2006), Xu et al. (2007) and Dai et al. (2014). However, the non-phreatophyte species, *N. tangutorum* and *C. mongolicum*, developed relatively shallow root systems (Fig. 3b and c). The abundant roots for these two species clustered mainly in the shallow or middle soil profile, indicating that water uptake from the upper soil profile or middle soil layer supplies the bulk of their water consumption. Due to plant age can affect the development of root structure (Cushman 1984; Laclau and Laclau 2009; Zanetti et al. 2015), further studies related to the effect of age on root morphology is required to fully understand the root functional type and water-use strategy of these shrubs.

In our study, a relative low night-time root water uptake in three desert shrubs was measured (Figs 6 and 7). Generally,

Table 4: Kendall's tau correlation matrix between root water uptake and the environmental variables

	RWU	PAR	VPD	Ta	Rain	Ts	Hs	V	D
<i>H. ammodendron</i>	Whole time	0.90**	0.64**	0.66**	−0.14**	0.29**	0.00	0.37**	0.13**
	Night-time	—	0.44**	0.50**	−0.10**	0.39**	0.10**	0.27**	0.07**
<i>N. tangutorum</i>	Whole time	0.82**	0.58**	0.61**	−0.10**	0.24**	0.15**	0.32**	0.10**
	Night-time	—	0.48**	0.43**	−0.06**	0.34**	0.10**	0.33**	0.02
<i>C. mongolicum</i>	Whole time	0.88**	0.65**	0.69**	−0.13**	0.38**	0.09**	0.36**	0.20**
	Night-time	—	0.61**	0.64**	−0.11**	0.52**	0.23**	0.28**	0.09**

Values with double asterisks mean that the correlation between root water uptake and environmental variables was extremely significant ($P < 0.01$).

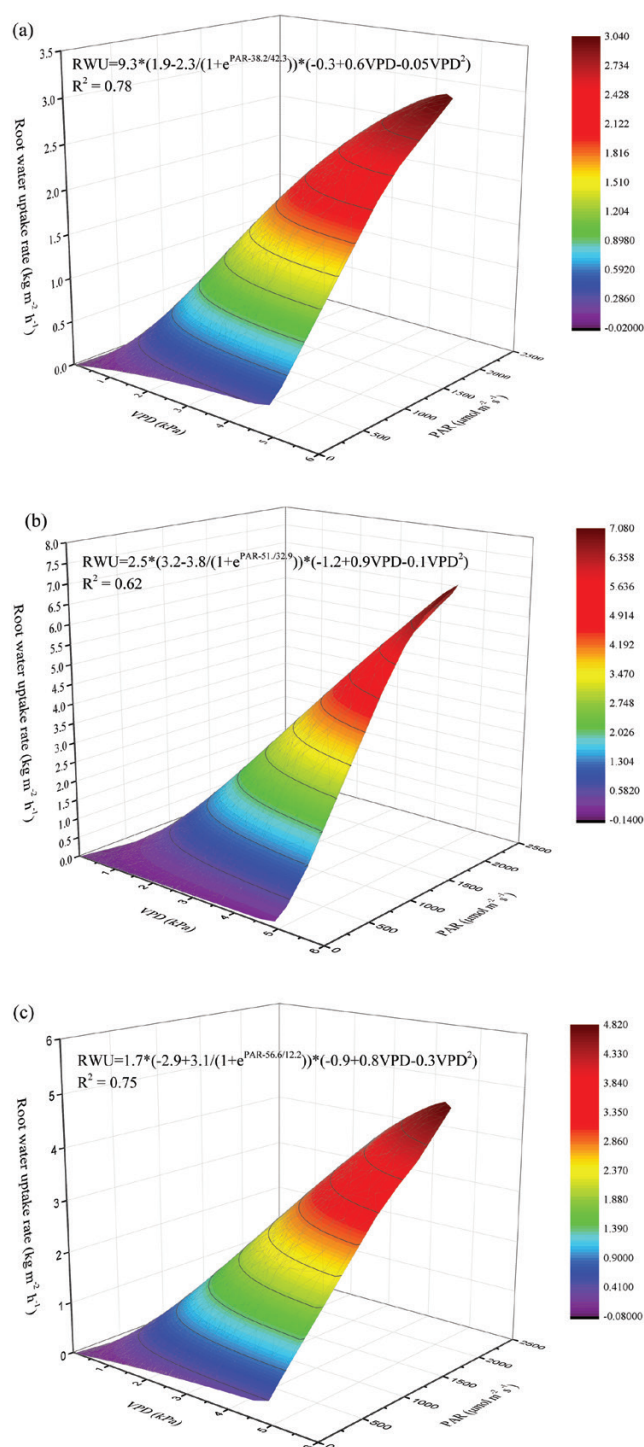


Figure 9: hourly estimated RWU rate response to instantaneous values of photosynthetic active radiation and VPD for *H. ammodendron* (a), *N. tangutorum* (b) and *C. mongolicum* (c).

the night-time water uptake could be a result of actual night-time transpiration of the canopy and/or water hydraulic redistribution (HR) (Deng *et al.* 2015). HR has been described in a wide variety of ecosystems and involves a wide range of life forms (Iván *et al.* 2010), defined as the passive movement

of water from wet soil to dry soil through root, driven by gradients in soil water potential (Burgess *et al.* 1998; Richards and Caldwell 1987). In arid environment, the passive movement of water usually takes place between deep, wet soil layers and upper, dry soil layers (Iván *et al.* 2010; Richards and Caldwell 1987).

However, we did not measure night-time canopy leaves transpiration. So, the contribution of night-time transpiration and HR to water uptake could not be distinguished. While according Deng's *et al.* (2015) study on *Hedysarum scoparium*, a desert shrub lived in semiarid northwestern China, the night-time water loss by canopy leaves was only 1.67% of the total night-time water consumption. We can reasonably presumed that the night-time water consumption of these desert shrubs was mainly used for water redistribution. Therefore, these species may utilize deeper soil water and even the shallow groundwater with the facilitation of the HR, especially for *H. ammodendron*, though their roots mainly occurred in the shallow or middle soil profile (Fig. 3).

Many studies suggested that soil water content play an important role in the plant water use (Harris *et al.* 2004; Jarvis *et al.* 1976; Stewart 1988; Wright *et al.* 1995; Whitley *et al.* 2008, 2009; Wang *et al.* 2014). For these desert shrubs, however, our results found a weak relationship between RWU and soil moisture (0–20 cm depth) (Table 4, Fig. 8). For phreatophytic species, *H. ammodendron*, there are only a few active roots occurred at the surface soil. Though non-phreatophytic species, *N. tangutorum* and *C. mongolicum*, allocated a relative high proportion of roots at the surface soil, their root water uptake at this depth is effective only when the rainfall event occurred (Chimner and Cooper 2004; Xu and Li 2006; Xu *et al.* 2007; Zhou *et al.* 2015). Therefore, the soil moisture had a weak effect on the RWU for three species. In addition, we cannot obtain soil moisture data for whole root zone due to the limited TDR gauges, which may cause uncertainties (Schulze *et al.* 1996; Wang *et al.* 2016).

CONCLUSIONS

This study examined the water-use strategy of three dominant desert species in northwestern China by measuring RWU rates during the summer using sap flow meters and excavating the intact root systems. Our results indicate that (1) the root functional type of *H. ammodendron* is phreatophytic, while *N. tangutorum* and *C. mongolicum* are non-phreatophytic, (2) *H. ammodendron* mainly uses middle-depth and deep soil water or some groundwater, *N. tangutorum* mainly uses shallow and middle-depth soil water, and *C. mongolicum* mainly uses shallow soil water and (3) the diurnal and seasonal dynamics of root water uptake in three species were significantly different, and closely related to environmental variables, especially to photosynthetic active radiation and VPD. These results suggested that the three species have distinct

water-use patterns, which may alleviate water competition during long-term water shortages.

Further research on horizontal distribution of root system is required to fully understand the root functional type of these shrubs at the scale of the individual plant. Detailed study of soil texture, variation of soil and xylem water potential and stomatal behavior under different weather is necessary for further understanding the characteristic of root water uptake of these plants. Integrated research on both will lead to complete understanding of the water-use strategy of these desert shrubs, and help to predict their success in future species competition.

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