Optimal root system strategies for desert phreatophytic seedlings in the search for groundwater

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Abstract: Desert phreatophytes are greatly dependent on groundwater, but how their root systems adapt to different groundwater depths is poorly understood. In the present study, shoot and root growths of *Alhagi sparsifolia* Shap. seedlings were studied across a gradient of groundwater depths. Leaves, stems and roots of different orders were measured after 120 days of different groundwater treatments. Results indicated that the depth of soil wetting front and the vertical distribution of soil water contents were highly controlled by groundwater depths. The shoot growth and biomass of *A. sparsifolia* decreased, but the root growth and rooting depth increased under deeper groundwater conditions. The higher ratios of root biomass, root/shoot and root length/leaf area under deeper groundwater conditions implied that seedlings of *A. sparsifolia* economized carbon cost on their shoot growths. The roots of *A. sparsifolia* distributed evenly around the soil wetting fronts under deeper groundwater conditions. Root diameters and root lengths of all orders were correlated with soil water availabilities both within and among treatments. Seedlings of *A. sparsifolia* produced finer first- and second-order roots but larger third- and fourth-order roots in dry soils. The results demonstrated that the root systems of desert phreatophytes can be optimized to acquire groundwater resources and maximize seedling growth by balancing the costs of carbon gain.

Keywords: desert phreatophytes; root system strategy; groundwater depth; soil water; biomass partition

Groundwater is crucial for desert phreatophytes in arid and semi-arid environments owing to poor precipitation and high evapotranspiration (Cui and Shao, 2005; Naumburg et al., 2005). Spatial heterogeneity and temporal fluctuation of groundwater tables influence water supply for these groundwater-dependent plants (Horton et al., 2001; Padilla and Pugnaire, 2007), and cause spatial vegetation diversity and temporal community changes (Stromberg et al., 1996; Rains et al., 2004). Groundwater extraction for agricultural or industrial use can potentially lead to strong fluctuation or permanent decline of groundwater tables in these areas (Elmore et al., 2006), and consequently result in water limitations or ultimately mortality for groundwater-dependent plants, if their root growth fails to follow the declining groundwater table (Horton and Clark, 2001; Elmore et al., 2006; Imada et al., 2008; Gui et al., 2013). Desert phreatophytes with large root systems in hyper-arid environments often experience water limitations owing to rare groundwater recharge

(Thomas et al., 2006; Bruelheide et al., 2010). Although a wealth of information has contributed to our understanding of relationship between groundwater and phreatophytes (Stromberg et al., 1996; Horton and Clark, 2001; Horton et al., 2001; Gries et al., 2003; Cooper et al., 2006; Thomas et al., 2006; Zeng et al., 2006; Bruelheide et al., 2010; Li et al., 2010), there is limited knowledge of the response of perennial desert plants to groundwater levels, especially from the perspective of the root system.

In water-limited areas, root systems play a vital role in sustaining desert phreatophytes (Rundel et al., 1991). Perennial desert phreatophytes growing in deserts greatly rely on developing deep root systems which enable them to tap deep soil water or groundwater resources (Thomas et al., 2006). For successful establishment, deep and fast root system development is especially necessary to access groundwater or to follow declining groundwater tables (Vonlanthen et al., 2011; Gui et al., 2013). In this case, optimization of biomass accumulation and root system development should be key strategies for desert plants to ensure early succession in unfavorable environments (Markesteijn and Poorter, 2009; Vonlanthen et al., 2011). Unlike the determining effects of groundwater on desert plants, little is known about how desert plant root systems respond to groundwater tables and what their main optimizing strategies are.

Root growth varies among heterogeneous soil patches (Eissenstat et al., 2000). Variation in root systems may greatly influence the efficiency of resource acquisition (Eissenstat, 1997; Comas and Eissenstat, 2004; Wang et al., 2013). Lateral fine root branches are both morphologically and physiologically responsive to changes in water availability (Pregitzer, 2002; Hodge, 2004; Comas et al., 2013). Drought affects the functioning of thinner roots and the mean specific root length (SRL) will decrease under soil dehydration, but not significantly (Ostonen et al., 2007). With increased drying of soils, and for different species, root diameter may increase (e.g. *Quercus frainetto* and *Q. ilex* in controlled environments; Manes et al., 2006), stay constant or decrease (e.g. *Picea abies* and *Pinus sylvestris* seedlings; Bartsch, 1987). The response of roots to water availability might be more complex by the simultaneous limitations of indispensable nutrients

and assimilates (Hodge, 2004). Although more generally present, the responses of roots to water availability were paid less attention compared to that of nutrient availability (Comas et al., 2013). Additionally, roots of different orders (distal unbranched roots as first-order roots, as classified by Pregitzer (2002) vary greatly in morphology, anatomy and physiology, which consequently leads to their divisions of functions on resource absorption, storage and transportation (Pregitzer, 2002; Wang et al., 2013). How roots of different orders respond to water availability is insufficiently understood. We know theoretically that finer roots are facilitated in resource acquisition by less carbon cost in resource-limited conditions and simultaneously possess non-conservative strategies with shorter longevities (Yanai et al., 1995; Eissenstat et al., 2000). However, this requires more evidence on multiple species. Moreover, the issue of whether higher-order roots have similar responses to lower-order roots does not yet have an answer.

Therefore, the aim of the present study is to reveal whether there are optimizing ways for desert phreatophytic seedlings to search for groundwater. We hypothesize that: (1) seedlings under deeper groundwater conditions will concentrate assimilation products to develop root systems, and will have faster vertical root growth and deeper distributed roots to extensively ensure their succession; and (2) to promote water uptake at less carbon cost, first- and second-order lateral roots, as well as higher-order roots, will be smaller and thinner (with higher SRL) in dry soils.

We used *Alhagi sparsifolia* Shap. (Leguminosae), one of the main natural perennial desert phreatophytes dominant in the southern Taklimakan Desert edge (Thomas et al., 2006), as our experimental material. Natural *A. sparsifolia* is greatly dependent on groundwater by forming monospecific stands at a large distance (about 16 m) to the groundwater (Arndt et al., 2004; Thomas et al., 2006, 2008). In both oasis foreland and inner sandy deserts with groundwater depths of 1–15 m (Vonlanthen et al., 2010), *A. sparsifolia* is crucial in supporting the fragile ecosystem and functioning as a shelter against drifting sand and as a main fodder for sheep (Zeng et al., 2002; Li et al., 2013). Nevertheless, the appearance of *A. sparsifolia* in these areas is reducing due to a lack of regeneration

and seedling succession, probably driven by less flooding and declines in groundwater (Gui et al., 2013; Li et al., 2013). In view of the key role and recent plight of *A. sparsifolia*, we chose seedlings of this species to test our hypotheses.

1 Materials and methods

1.1 Study area

The research was carried out at the Cele National Station of Observation and Research for Desert Grassland Ecosystem (37º00.97N', 80º43.77'E; 1,365 m asl), located in the southern Taklimakan Desert edge. The extreme continental climate in the study area is characterized by cold, dry winters and hot, dry summers with rare annual precipitation, usually less than 35 mm, and high annual potential evaporation of over 2,590 mm (Arndt et al., 2004; Bruelheide et al., 2010). The maximum temperature in this area reaches to 42°C in summer, and the minimum temperature is as low as −24°C in winter (Tomas et al., 2006). The soils are very uniform with more than 87% of silt. Constrained by water resources, the region is covered by sparse desert vegetation. The predominant natural species are *A. sparsifolia*, *Tamarix ramosissima* Ledeb., *Populus euphratica* Oliv., *Phragmites australis* (L.) Steud. and *Karelinia caspia* (Pallas) Lessing (Zeng et al., 2006; Vonlanthen et al., 2010).

1.2 Experimental design

Seedlings were first seeded in plastic cultivation cups (15-cm high, 8-cm diameter) for 15 d (10–24 April 2012). The cups were filled with sandy loam soil (soil properties: air-dry water content was 0.67%, field capacity 24.52%, capillary capacity 20.49% and average bulk density 1.36 g/cm^3) collected from the local desert environment and screened by a fine mesh. At the beginning of the transplantation, the average height and taproot length of *A. sparsifolia* seedlings were 5.50±0.90 and 10.70±1.20 cm, respectively.

Seedlings of similar growth status were selected and transplanted into cultivation soil containers (1 m×1 m, see Figs. 1a and b) with different simulated groundwater tables (40, 80, 120, 180 and 220 cm). For increasing the possibility of root appearance in root observation windows (Fig. 1c), we transplanted five seedlings in the center and diagonals of each cultiva-

tion soil container, respectively (Fig. 1b, circles in the inset quadrat were the seedling's locations).

Soil containers were carefully prepared and filled with the same sandy loam soils used in the cultivation cups before the transplantation. For getting a stable soil condition (such as soil moisture and compactness) in different layers, we added water through the pipes (Fig. 1d) at the 15th day before seedling transplantation and kept the groundwater table in a fixed level (about 0.6 m apart from the base). By adding water daily, a stable soil wetting front (i.e. an obvious boundary between wet and dry soils) appeared in the observation window owing to the capillary lift, indicating a less variable vertical soil water profile in each soil container.

After transplantation, seedlings were irrigated with 100 mL of freshwater per plant every morning from 25 April to 11 May, and then the irrigation period decreased to every other day during 12–27 May. Later on, we stopped irrigation and started the groundwater table treatment. The groundwater table was kept at a nearly constant level for 120 d (28 May to 26 September) by adding water every morning. According to the different sets of soil containers, we obtained five groundwater table treatments with different depths of 40, 80, 120, 180 and 220 cm (WT40, WT80, WT120, WT180 and WT220, respectively). Each water table treatment had three replicates. Because of root penetration to the level of groundwater before the water table treatment was applied, the WT40 treatment was abandoned.

1.3 Measurements

According to the vertical profiles of soil water attributes, we divided every 20-cm depth as a soil layer. The depth of wetting front in each soil container was recorded every 30 d after the groundwater treatments. Soil gravimetric water contents of each layer were measured by CNC100 neutron moisture gauge (Beijing Nuclear Instrument Corp., Beijing, China) with an iron pipe (4 cm in diameter) in container of each treatment after 30, 60, 90 and 120 d of the groundwater treatments.

Plant height and canopy diameter (the average of diameters in each of the cardinal directions) were measured every 15 d by ruler (precision of 0.1 cm) to determine the height growth rate (HGR) and canopy
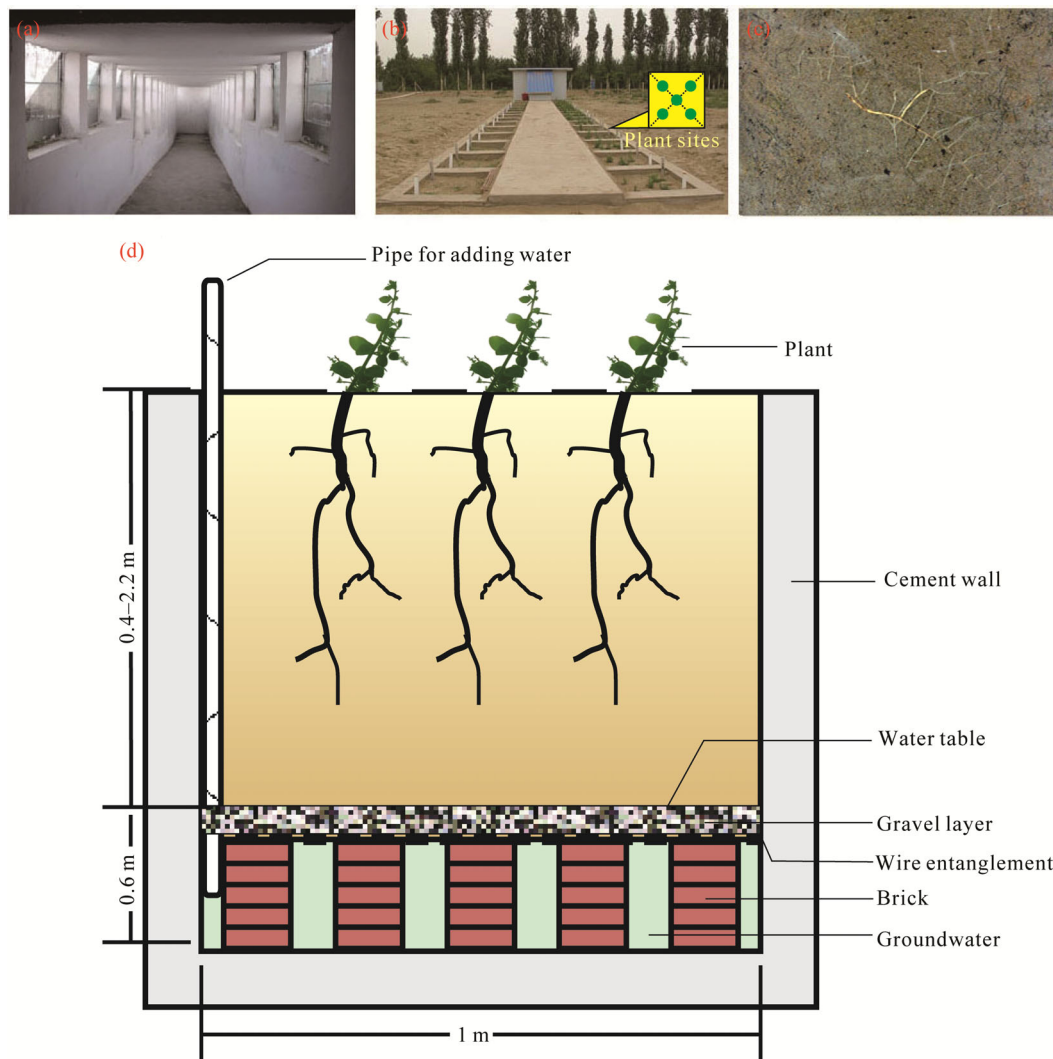
Fig. 1 Details for cultivation containers. a, inside view; b, outside view; c, glass windows for root observation; d, structure design of cultivation containers: each container consisted of three cement walls and one glass window for root observation. Gravel layer, wire entanglement and bricks help to prevent soil particles falling into the simulated groundwater. The water table was kept at a fixed level (0.6 m from the base of the container) by frequently adding water from the pipe.

diameter growth rate (CDGR). Root growth tracks reflected by the observation windows were marked by different colors every 10 d. The new growth of root length during the 10 d was measured to determine the root growth rate (RGR). We checked root access to groundwater through the observation windows daily to determine the exact time period of roots accessing groundwater (TP). If the root accessed the groundwater, we calculated the rooting depth growth rate (RDGR) of this treatment during this period by the following equation: RDGR=(rooting depth–initial root length)/TP. If the root did not access the groundwater, we measured the final rooting depth of each treatment

at harvest time to calculate RDGR. During the treatment period, only roots in the WT220 treatment did not access the groundwater.

At the end of the treatments, all leaves, stems and roots of different orders were harvested for the determination of biomass, leaf area, leaf thickness (LT), root length (RL) and root diameter (D). From each harvested individual, we divided the aboveground parts into leaves and stems. All leaves and stems were sub-packaged with envelopes for further determination of stem mass, leaf mass and total leaf area (TLA). For the determination of LT, area per leaf (APL) and specific leaf area (SLA), 10 mature leaves of every in-

dividual in each soil container were selected separately. Ten overlaid leaves were measured six times using an electronic digital caliper (precision of 0.01 mm) to calculate the average LT. We used DT-scan software (Delta-T Devices, Cambridge, UK) to calculate the leaf area from the images scanned by FileScan 1660XL scanner (Microtek Technology Co., Shanghai, China). Scanned leaves and stems were sub-packaged, oven-dried at 75°C for at least 48 h and weighed for total biomass. SLA was calculated by the following equation: SLA=leaf area/leaf dry mass.

We dug out all roots in each soil layer (every 20 cm was a soil layer) using shovels and rakes. We distinguished fresh and dead roots by their color, since fresh roots of *A. sparsifolia* were white, while dead ones were brown or black. The fresh roots collected from each layer were sub-packaged in plastic bags with water. We classified roots by order beginning with distal unbranched roots as first-order roots (described by Pregitzer et al. (2002)). Fresh roots in different soil layers were scanned by a high-precision scanner (FileScan 1660XL) to get root images for further analysis. We added up root lengths of the same order in all soil layers to show the difference of root lengths by order for the different treatments. Here, $RL_{1,2}$ is the length of first- and second-order roots in all soil layers. RL_3 is the length of third-order roots. RL_4 is the length of fourth-order roots. TRL is the total root length of all orders. After scanning, all roots in different layers were sub-packaged in envelopes, oven-dried at 75°C for at least 48 h and weighed for dry mass using elec-

tronic analytical balance (JA5003, Shanghai Balance Instrument Plant, China) with precision of 0.1 mg. SRL was calculated by the following equation: SRL=root length/root dry mass.

1.4 Data analysis

Variables of biomass partitioning, leaf and root morphology and relative growth were examined; the abbreviations and units used for these variables are summarized in Table 1. Herein, total biomass is the sum of leaf, stem and root dry mass. Shoot mass is the sum of leaf and stem dry mass. Leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR) are the ratio of leaf mass, stem mass and root mass to total biomass, respectively. Root/shoot ratio (R/S) is the ratio of root mass to shoot mass. Root length/leaf area ratio (RLA) is the ratio of total root length to leaf area. First- and second-order roots constitute absorptive ephemeral root modules of *A. sparsifolia*, while higher-order roots possess xylem and vascular bundles with functions of mechanical support, resource transportation and storage. Thus, we classified the first- and second-order roots as absorptive roots for further analysis of the proportion of absorptive roots (PAR).

Data were analyzed using SPSS 16.0 software (SPSS Inc., Chicago, IL, USA) and plotted by EXCEL 2010 (Microsoft Software, Redmond, WA, USA) and Origin 8.0 (Microcal Software, Northampton, MA, USA). We determined the significance of variable variances in different treatments using one-way analysis of variance (ANOVA) and Tukey's HSD test. For

Table 1 Variables of biomass partitioning, leaf or root morphology and relative growth responses with abbreviations and units

Variable	Abbreviation	Unit	Definition
Height growth rate	HGR	cm/d	Height growth per day
Canopy diameter growth rate	CDGR	cm/d	Canopy diameter growth per day
Rooting depth growth rate	RDGR	cm/d	Rooting depth growth per day
Leaf mass ratio	LMR	g/g	Leaf biomass per total biomass
Stem mass ratio	SMR	g/g	Stem biomass per total biomass
Root mass ratio	RMR	g/g	Root biomass per total biomass
Root/shoot ratio	R/S	g/g	Ratio of root dry biomass to shoot dry biomass
Proportion of absorptive root	PAR	g/g	Ratio of absorptive root biomass to total root biomass
Root length/leaf area ratio	RLA	cm/cm^2	Ratio of root length to leaf area
Specific leaf area	SLA	mm^2/mg	Leaf area per leaf biomass
Specific root length	SRL	m/g	Root length per root biomass

analyzing the vertical distribution of roots, we fitted the total RL and biomass by depth sections to the asymptotic regression equation $Y=1-\beta^d$, where Y was the cumulative root biomass or length fraction, summed up from the surface to the depth d, and the regression coefficient β indicated the steepness of declining root proportions with depths (Vonlanthen et al., 2010). Linear fittings of root diameter and SRL were done to examine their responses to water availability. Before fitting, parameters were ln-transformed to better linearize the regression.

2 Results

2.1 Soil moisture profiles

The depth of soil wetting front and vertical distribution of soil water content in the experiment were controlled by the groundwater table of each treatment (Figs. 2 and 3). The depths of soil wetting front in the groundwater treatments of WT80, WT120, WT180 and WT220 were 14, 43, 88 and 116 cm, respectively (Fig. 2), and seldom changed throughout the treatment period. Soil water content of the same layer in the deeper groundwater treatment was lower, indicating poor water availability. Soil water contents in the shallow soil layers of WT80 and WT120 treatments increased after 60 d of cultivation, while those at WT180 and WT220 treatments decreased. The soil water contents in the basal soil layers (about 21%; Fig. 3) were nearly constant through the whole treatment period. Soil water contents near the wetting fronts for WT80 and WT120 treatments increased over time, while those for WT180 and WT220 treatments changed little.

2.2 Aboveground and underground growths

The different groundwater table treatments had opposite effects on aboveground and underground growth rates (Table 2). HGR for WT220 treatment was significantly lower than those for WT80 and WT120 treatments ($P<0.05$). CDGR for WT220 treatment was non-significantly ($P>0.05$) lower than those for other treatments. Although more time was needed for plant roots to access groundwater in deeper groundwater treatments, RDGR and RGR were significantly higher ($P<0.05$) for WT180 and WT220 treatments than those of other treatments.

Total biomass, leaf biomass, stem biomass and TLA of *A. sparsifolia* seedlings decreased across an increasing gradient of groundwater table depths (Figs. 4a and c), indicating negative impacts on plant growth to the depths of groundwater. The root biomass for WT180 was significantly greater than those for WT80 and WT220 treatments ($P<0.05$), while there were no significant differences in root biomass between WT120 and other treatments. There were no significant differences in TRL, $RL_{1,2}$, RL_3 and RL_4 (Fig. 4b) among different treatments ($P>0.05$).
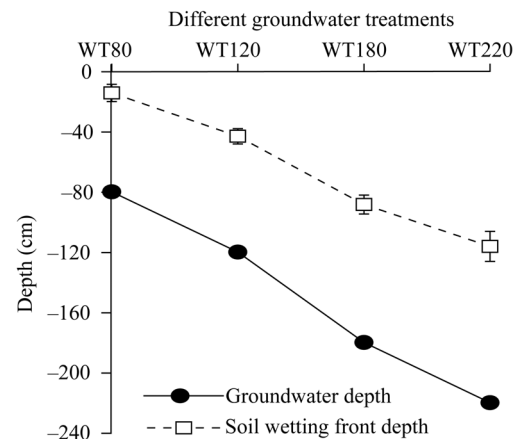

Fig. 2 Depths of soil wetting fronts in different groundwater treatments. Error bars represent standard errors of single measurement in six replicates.

Table 2 Growth rates of *A. sparsifolia* in different groundwater treatments

Treatment	HGR (cm/d)	CDGR (cm/d)	TP (d)	RDGR (cm/d)	RGR (cm/d)
WT80	0.34±0.11[a]	0.89±0.14[a]	81±4[b]	0.86±0.04[d]	0.66±0.15[c]
WT120	0.39±0.15[a]	1.08±0.35[a]	84±3[b]	1.30±0.04[c]	1.05±0.41[b]
WT180	0.27±0.08[ab]	1.01±0.36[a]	89±3[b]	1.90±0.66[a]	1.44±0.09[a]
WT220	0.19±0.10[b]	0.80±0.18[a]	123±6[a]	1.70±0.87[b]	1.50±0.14[a]

Note: HGR, height growth rate; CDGR, canopy diameter growth rate; TP, time period for roots to access groundwater; RDGR, rooting depth growth rate; RGR, root growth rate. Different lowercase letters indicate significant difference at $P<0.05$ among different treatments.
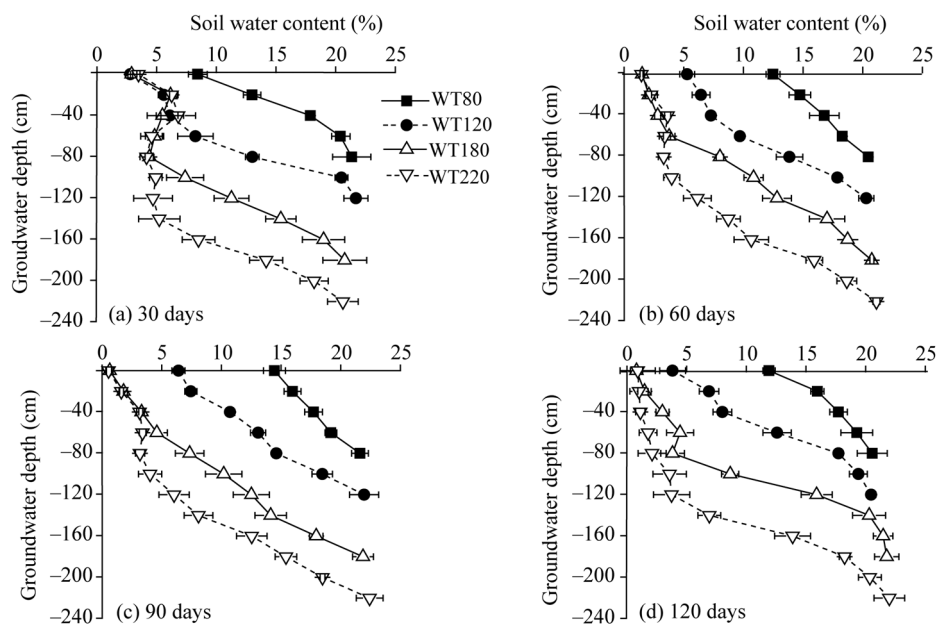
Fig. 3 Soil water contents under different groundwater depths after 30 (a), 60 (b), 90 (c) and 120 (d) days treatments. Error bars represent standard errors of single measurement in six replicates.

2.3 Biomass partitioning and morphological changes

There were significant differences in biomass partitioning and leaf morphology among all treatments (Table 3). LMR and SMR were significantly higher for W80 and WT120 treatments than those for WT180 and WT220 treatments, while the values of RMR, R/S and RLA were lower. Individual plants growing in treatments with deeper groundwater tables allocated more biomass to roots. The PAR did not vary significantly among all treatments, maintaining a constant proportion (about 50%) of root biomass. Individual plants for the WT180 and WT220 treatments produced smaller and thicker leaves with lower SLA, but showing no significant difference in LT.

2.4 Vertical root distribution

Vertical distribution of both total RL and biomass showed differences among different treatments (Fig. 5 and Table 4). Across an increasing gradient of groundwater tables, *A. sparsifolia* seedlings developed more deeply even-distributed roots (significantly larger β, $P<0.01$). More than 93.0% of the total root biomass and 81.7% of the total RL in the WT80 treatment were distributed in the soil depth of <60 cm. Unlike the WT80 and WT120 treatments, where seedlings mainly developed roots in subsoil, seedlings in the WT180 and WT220 treatments developed much deeper root systems (with significantly larger β, $P<0.01$) and mainly concentrated roots in middle soil

Table 3 Parameters of biomass partitioning and leaf morphology in different groundwater treatments

Treatment	Biomass partition						Leaf morphology		
	LMR (g/g)	SMR (g/g)	RMR (g/g)	PAR (g/g)	R/S (g/g)	RLA (cm/cm^2)	APL (cm^2)	LT (mm)	SLA (mm^2/mg)
WT80	0.24±0.02^a	0.48±0.04^a	0.29±0.06^b	0.53±0.04^a	0.41±0.13^b	1.41± 0.32^b	0.80±0.02^{ab}	0.23±0.01^a	9.42±0.26^b
WT120	0.21±0.00^{ab}	0.41±0.02^a	0.39±0.03^b	0.50±0.03^a	0.64±0.08^b	1.88±0.07^b	0.85±0.03^a	0.24±0.00^a	10.80±0.54^a
WT180	0.17±0.01^b	0.24±0.01^b	0.60±0.03^a	0.49±0.03^a	1.49±0.15^a	3.34±0.40^a	0.74±0.04^b	0.25±0.00^a	9.04±0.23^{bc}
WT220	0.16±0.03^b	0.29±0.03^b	0.55±0.06^a	0.49±0.01^a	1.25±0.28^a	3.54±0.80^a	0.64±0.03^c	0.27±0.01^a	8.35±0.14^c

Note: LMR, leaf mass ratio; SMR, stem mass ratio; RMR, root mass ratio; PAR, proportion of absorptive root biomass; R/S, ratio of root to shoot biomass; RLA, ratio of root length to leaf area; APL, area per leaf; LT, leaf thickness; SLA, specific leaf area; Different lowercase letters mean significant difference at $P<0.05$ among different treatments.
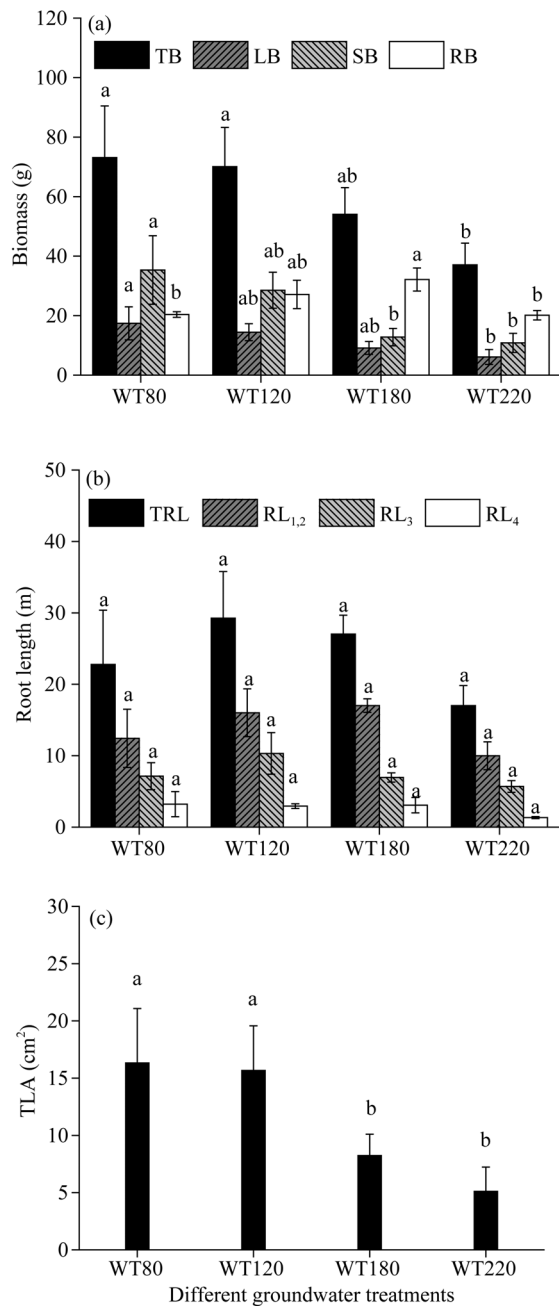
Fig. 4 Average values of biomass (a), root length (b) and leaf area (c) under different groundwater treatments. TB, total biomass; LB, leaf biomass; SB, stem biomass; RB, root biomass; TRL, total root length; $RL_{1,2}$, first- and second-order root length; RL_3, third-order root length; RL_4, fourth-order root length; TLA, total leaf area. Different lowercase letters indicate significant difference at $P<0.05$ among different treatments.

layers of 60–140 cm (i.e. near the wetting fronts).

2.5 Relationship between root morphology and soil water content

There were significant correlations between soil water contents and root morphologies (ln-transformed linear fitting results, $P<0.01$) both in different soil layers within the same treatments and among all treatments (Fig. 6). Root diameters of first- and second-order roots ($D_{1,2}$) both within and among treatments were significantly correlated with soil water contents ($P<0.01$). There were larger first- and second-order roots in wet soils, and smaller ones in dry soils. The diameters of third-order roots (D_3) ($R^2=0.16$, $P<0.01$) and fourth-order roots (D_4) ($R^2=0.18$, $P<0.01$) were negatively correlated with soil water contents among all treatments, but the correlation was poor and there was no corresponding correlation within a single treatment. The values of D_3 for the WT220 treatment were poorly negatively correlated with soil water contents ($R^2=0.30$, $P<0.01$). The values of D_4 for the WT120 treatment ($R^2=0.36$, $P<0.01$) were positively correlated with soil water contents, while those values of D_3 and D_4 for other treatments were not significantly correlated ($P>0.05$). The specific root lengths of first- and second-order roots ($SRL_{1,2}$, except that of treatment W120) were significantly negatively correlated with soil water contents both within a single treatment and among treatments ($P<0.01$), while those of third-order roots (SRL_3) and fourth-order roots (SRL_4) were positively correlated with soil water contents.

3 Discussion

3.1 Groundwater effects on soil water and seedling growth

By controlling different but temporally-stabilized groundwater tables and using the same soil type with similar capillary suction ability in all treatments, we established a groundwater-controlled and slightly-changed vertical distribution of soil water contents over a duration of time. Declinations of soil water contents from topsoil to subsoil and visible constant soil wetting fronts were presented, mainly because of limited distance of capillary suction in subsoil and continuous evaporation in topsoil (Gerla, 1992). Slight increase of soil water content in topsoil of shallow groundwater treatments might be caused by the amplifying effect of hydraulic lifting by the enlarging root systems that exist in many plant species (Neumann
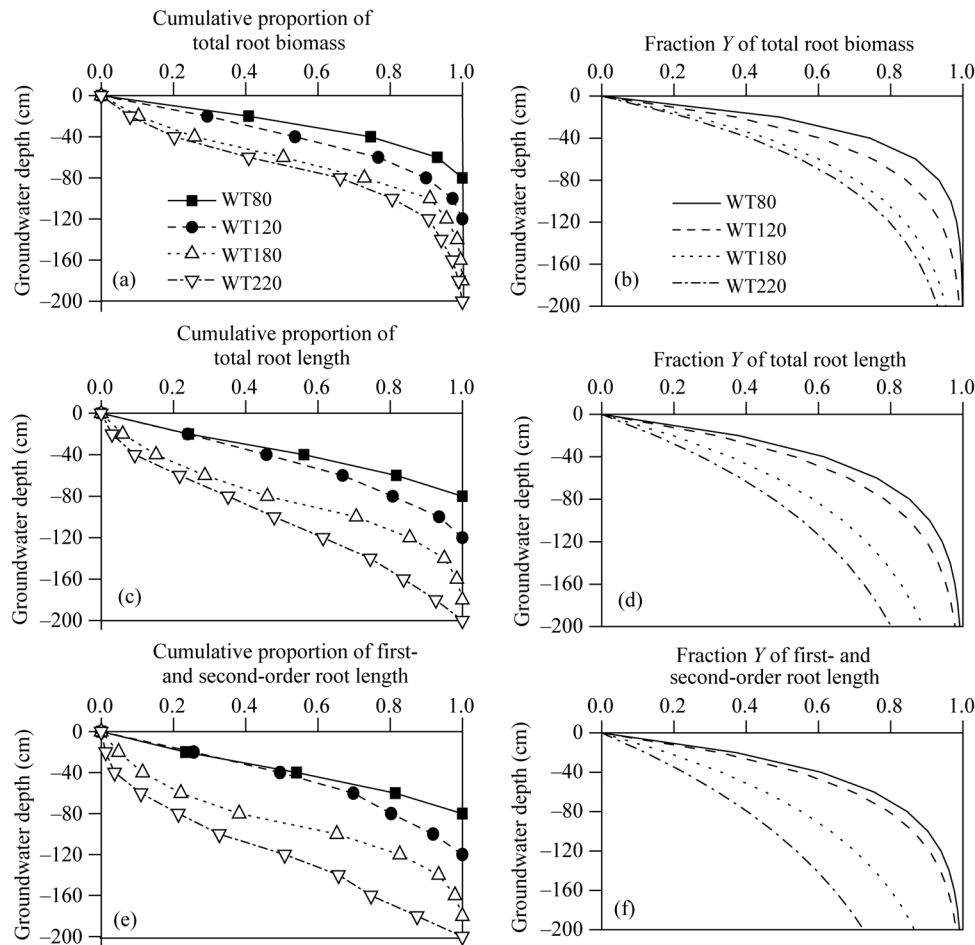
Fig. 5 Vertical distributions of root biomass (a), lengths (c and e) and their regression fitting results (b, d and f) under different groundwater depths. Fraction Y, calculated as proportion of cumulative root biomass or length, summed up from the soil surface to depth d, using the equation $Y=1-\beta^d$. The regression coefficient β indicates the steepness of declining root proportions with depths.

Table 4 Regression analysis of proportion of total root biomass or length using the equation $Y=1-\beta^d$ under different groundwater treatments

Treat-ment	Total root biomass				Total root length				First- and second-order root length			
	β	SD	R^2	F	β	SD	R^2	F	β	SD	R^2	F
WT80	0.967[c]	0.004	0.978	175.92	0.976[c]	0.001	0.930	53.10	0.977[b]	0.002	0.923	48.25
WT120	0.977[b]	0.003	0.974	221.27	0.981[b]	0.002	0.964	160.58	0.980[b]	0.002	0.976	239.18
WT180	0.985[a]	0.000	0.911	92.28	0.989[a]	0.000	0.861	55.57	0.990[a]	0.001	0.829	52.63
WT220	0.987[a]	0.000	0.912	103.44	0.992[a]	0.001	0.868	65.63	0.994[a]	0.001	0.795	38.72

Note: The regression coefficient β indicates the steepness of declining root proportions with depth d. Different lowercase letters indicate significant difference at $P<0.05$ among different treatments.

and Cardon, 2012). Furthermore, the increase in soil water content near the wetting front for shallow groundwater treatments can also be explained by the hydraulic lifting of plant root systems, while no significant changes of those with deep groundwater treatments might be caused by smaller and more deeply-distributed root systems with limited hydraulic

lifting abilities.

The effects of groundwater on growth of *A. sparsifolia* seedlings were consistent with early research result demonstrating that water availability has remarkable influences on plant growth, biomass accumulation and leaf morphology (Chaves, 1991; Chaves et al., 2003; Blum, 2011). In our study, across a declining gradient of
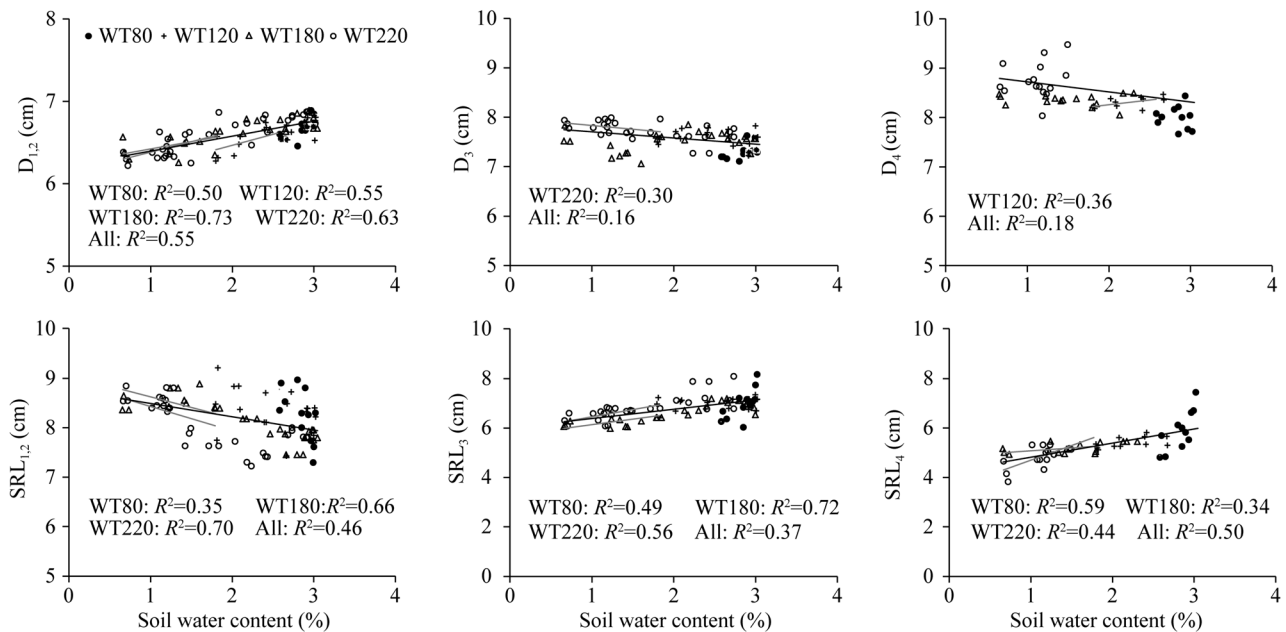
Fig. 6 Correlations of root diameters and specific root lengths with soil water contents (only significant results were shown, $P<0.05$). $D_{1,2}$, first- and second-order root diameter; D_3, third-order root diameter; D_4, fourth-order root diameter; $SRL_{1,2}$, specific root length of first- and second-order roots; SRL_3, specific root length of third-order roots; SRL_4, specific root length of fourth-order roots. All data were ln-transformed before linear fitting.

groundwater tables, it was harder for roots to reach adequate soil water depths. Without sufficient water supply, A. sparsifolia seedlings reduced the production of leaves under deeper groundwater conditions in order to reduce water consumption, and finally led to lower shoot growth rate and total biomass accumulation. More assimilation products of *A. sparsifolia* seedlings were allocated to underground to develop the root system for spatial exploitation and resource acquisition. These findings were in accordance with the optimal biomass partition strategy in which plants preferentially allocate biomass to acquire the resource that most limits their growth (Kobe et al., 2010). An adaptive strategy of leaf morphology was also shown in the present study. There were smaller, thicker leaves with lower SLAs for *A. sparsifolia* seedlings in deep groundwater conditions. A smaller leaf size to reach maturity was one constitutive pathway to reduce transpiration area and optimize energy use (Chaves et al., 2003). Meanwhile, thicker leaves with lower SLA as a result of an increased investment in structural tissues might allow increased resistance to unfavorable environmental conditions (Maroco et al., 2000). Thus, we may deduce that smaller and thicker leaves with lower SLAs in deep groundwater

conditions can partially compensate for the lower rates of carbon gain by investing less in new leaf construction.

3.2 Reinforcement of root system development to search for groundwater

Although the time period for roots to access the groundwater under deep groundwater conditions was longer, an acceleration of root growth and RDGR was found, reflecting the reinforcement of deep root system development to reach groundwater. Since more assimilation products were allocated to the root system, the reinforcement of root system development under water-limited conditions, which can be further recognized by RLA or R/S (Körner and Renhardt, 1987; Ryser and Eek, 2000; Blum, 2011), greatly enhances the plant's ability to balance water acquisition and consumption. Although hindrances to biomass accumulation and rooting depth growth of *A. sparsifolia* seedlings under condition with groundwater depth deep to 220 cm were shown, mainly caused by less water availability, its root growth and rooting depth were significantly higher than those with shallower depths of 80 and 120 cm. Similar to the results of Zeng et al. (2012) and Gui et al. (2013), finding that moderate water deficit promoted faster ver-

tical root elongation of *A. sparsifolia* seedlings, our study also demonstrated that the acceleration of root growth in deep groundwater conditions helped roots to reach the groundwater. In this way, we believe that the acceleration of root growth will benefit seedling succession in this hyper-arid environment.

3.3 Optimal root system response to water availability

Variations in root vertical distribution and morphology under different groundwater conditions reflect root systems optimized by balancing carbon cost and water uptake efficiency. On hydrological grounds, root distribution can be seen as a reflection of the plant's optimization strategy. The 'optimal' root distribution is the one which optimizes carbon cost and maximizes water uptake (Van Wijk and Bouten, 2001). In the present study, in contrast to seedlings in shallower groundwater conditions with roots mainly concentrated in topsoil above 60 cm, seedlings with deeper groundwater developed much deeper root systems and mainly concentrated first- and second-order roots in the depth around soil wetting fronts. These results suggested that roots of *A. sparsifolia* seedlings would proliferate at depths where there were favorable conditions for water. Seeking groundwater, *A. sparsifolia* seedlings developed much deeper root systems and proliferated absorptive roots in deep soil, and thus can exhibit superior performance in extracting water for maximizing growth. These results were similar to those of Vonlanthen et al. (2010) and Gui et al. (2013).

Diverse *A. sparsifolia* roots with different Ds and SRLs were produced depending on soil water conditions, reflecting balancing strategies for root system optimization. Since first- and second-order roots (third-order roots are included for some species) are ephemeral roots employed as absorptive modules for resource uptake (Xia et al., 2010), we believe that morphological changes and distribution of these roots give theoretical information concerning adaptive strategies on root system development response to water availability. Similar to previous studies by Yanai et al. (1995) and Wang et al. (2013), demonstrating that finer roots may facilitate the recent acquisition of resources in resource-limited soils by less carbon consumption, our study also found finer first- and second-order roots in dry soils that could extensively increase water uptake with less carbon cost.

Theoretical analysis has elaborated that the most efficient roots for resource uptake would be thin (with high SRL) (Yanai et al., 1995; Eissenstat, 1997), but they also have relatively shorter lifespans and weaker resistance to soil biotic stress (Luke McCormack et al., 2012). The present study showed that thinner first- and second-order roots proliferated in dry soils, in contrast, higher-order roots had a different pattern. Third- and fourth-order roots were relatively larger with lower SRL in dry soils. The discrepant response of higher-order roots might result from balancing carbon cost and root efficiency on transportation and proliferation rather than resource uptake abilities. It is possible that larger diameters would help higher-order roots to be maintained for longer and function as a producer of lower-order roots and as a resource transporter in dry soil conditions. If so, this would compensate for the carbon cost for the generation of new higher-order roots and perform as a more efficient resource transporter. In this way, the specific proliferation of diverse orders of roots with different morphologies in heterogeneous soils would benefit the optimization of plant resource acquisition and carbon cost for maximizing plant growth.

The proportion of absorptive roots (PAR) is also crucial for the absorption of water and nutrients, but the different classification methods of absorptive roots might lead to different results. By classifying fine roots with diameters less than 1 mm as absorptive roots, early research on *Populus alba* juvenile trees showed that PAR decreased with deeper water table depths, and it was one optimal strategy in response to water limits (Imada et al., 2008). However, our study did not show any evidence of this kind of strategy by classifying first- and second-order roots as absorptive roots.

4 Conclusions

Groundwater depths are crucial for seedling growth of desert phreatophytes. Our study aimed to determine whether there were optimal root system strategies for desert phreatophytes in the process of their search for groundwater. The results showed that *A. sparsifolia* seedlings in different groundwater conditions had optimal root system strategies by balancing carbon cost and functional efficiency. Deep groundwater tables induced more biomass to be allocated to root systems and much faster root growth, as well as rooting depth growth, which would benefit the spatial exploitation of

root system in the search for water. Roots were more deeply extended in the humid soil depths around wetting fronts for maximizing the water uptake. Variation in root morphologies at different groundwater tables reflected optimal root proliferation strategies. For example, finer first- and second-order roots with higher SRLs in drier soils facilitated resource absorption with less carbon consumption. However, in contrast with our second hypothesis, higher-order roots were larger with lower SRLs. Although we did not determine the lifespans of the roots of diverse morphology, which will be determined in future studies, we believe that larger higher-order roots will benefit the production of lower-order roots and function in resource transportation, and provide an advantage due to less carbon cost required for construction of new higher-order roots.

Despite a huge body of literature showing groundwater depths limit seedling growth and succession of phreatophytes, this study shows that the seedlings of desert phreatophytes may accelerate vertical root elongation growth and optimize root system construction by balancing carbon cost and resource uptake, which consequently alleviate water limitations for desert seedling succession. Moreover, the findings of diverse morphology of roots of the same order in different soil layers with discrepant water availabilities should attract more attention to precise root system sampling and observation in future research.

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