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South African Journal of Botany

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

Patterns of root architecture adaptation of a phreatophytic perennial desert plant in a hyperarid desert

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ARTICLE INFO

Article history:

Received 3 September 2012

Received in revised form 21 January 2013

Accepted 5 February 2013

Available online 6 March 2013

Edited by J Van Staden

Keywords:

Alhagi sparsifolia Shap

Phreatophytic perennial plant

Root architecture

Root biomass

ABSTRACT

Plant root systems can respond to nutrient availability and distribution by changing the three-dimensional deployment of their root architecture. The year after year variation of root architecture was investigated in a perennial phreatophyte in the controlled condition vegetation situated in the oasis in the Chinese Taklamakan desert with the goal to elucidate their adaptation to hyperarid environment. The whole plants of an indigenous perennial legume *Alhagi sparsifolia* Shap. with intact root systems were excavated at the end of each growing season from 2007 to 2009 and analyzed for architecture, above and belowground biomass, root/shoot ratio, root depth, seed yields and ramet. Changes in water availability were found to have stupendous effects on taproot depth, lateral root length and ramet quantity. Relative to shoot dry weight, taproot depth decreased with increasing water availability. In contrast, lateral root elongation was promoted by higher water availability.

We tested the hypothesis that (1) irrigation increases root biomass and the quantity of ramets, and (2) *A. sparsifolia* Shap. develops an efficient root architecture that could absorb soil water and nutrition.

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1. Introduction

Alhagi sparsifolia Shap. (camelthorn, Fabaceae) is a spiny, perennial phreatophytic herb with few leaves, about 1 m tall (Zeng and Liu, 2012). Shoots die off completely each winter and regenerate again in spring (Rzepecki et al., 2011). In an environment with 35 mm annual precipitation, where all dominant indigenous plant species in the foreland are phreatophytes (Gries et al., 2003; Rzepecki et al., 2011), groundwater is the only predictable and stable water source for all vegetation types in the oasis foreland (Arndt et al., 2004; Foetzki, 2004; Gries et al., 2005; Zeng et al., 2006; Bruelheide et al., 2010).

In washy years, some flood is distributed draining into the desert through a system of ancient and recent river-basins, but in dry years the river water is completely directed through the oasis and used for field irrigation, with the remainder draining into the desert (Gries et al., 2005). Now, more and more barrages or reservoirs are built in upstream for storing summer floodwater in order to irrigate arable fields in spring. The accounts and opportunities of floodwater overflowed to the transition zone between the oases and the open silt desert are

gradually reduced leading to a sharp decline in the groundwater level, and the landscape of Cele oasis has considerably changed in the past 50 years due to natural dominant vegetation degradation by human overuse (Bruelheide et al., 2003). The width of the indigenous vegetation belt seriously decreases resulting from the advancing desert and the expansion of arable land (Bruelheide et al., 2010), and this will make the process of protective vegetation restoration become more difficult (Gries et al., 2005).

Sheep, goats, rabbits, donkeys, camels and other mammals enjoy browsing and grazing *A. sparsifolia* Shap., which with high protein content, just due to the palatability, the appearance of *A. sparsifolia* Shap. in natural environment is greatly reduced. If the phreatophytes vanish there will be nothing left to stop the shifting sand encroachment of the oases (Bruelheide et al., 2003).

The rains are irregular and infrequent, sometimes with no rain during several years. Annual precipitation is insignificant for plant growth; and typically no water is stored in the soils down to the capillary fringe (Thomas et al., 2000). The natural germination of seeds is severely restricted by surface soil water content, so spontaneously emerging seedlings of *A. sparsifolia* Shap. are infrequent. Natural flooding is the only possible approach for regeneration of all occurring plant species (Bruelheide et al., 2003; Gries et al., 2005). Allocation of C to below-ground plant structures is one of the most important, yet least well quantified fluxes of C in terrestrial ecosystems (Kell, 2011; Wiley and Helliiker, 2012), although a significant amount of work has been done

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in quantifying root production (Fujii and Kasuya, 2008; Gaul et al., 2008; Huang et al., 2008).

Estimates of below-ground biomass are more difficult (Yu et al., 2012). At the same time, very limited information regarding root growth and production of hyperarid deserts is available (Polverigiani et al., 2011). There are many reasons for studying the root systems of different plants and various habitats (Nibau et al., 2008). The aim in this investigation is a better understanding of the rooting habits of certain hyperarid dwelling plant. Many plants can alter biomass allocation (Poorter et al., 2012), root: shoot ratios (Beets et al., 2007), plant rooting depths (Scholz et al., 2012) and root architecture (Hodge et al., 2009) or uptake capacity (Comas and Eissenstat, 2009) in response to low soil resource availability. However, virtually nothing is known about (a) the role of irrigation in the establishment process of seedlings, (b) the effect of irrigation on root biomass, and (c) the response of the seedlings after twice irrigation. To investigate the importance of irrigation we conducted an experiment in the transition zone between desert and oasis. We hypothesized: (1) irrigation would increase biomass and the quantity of ramets, and (2) *A. sparsifolia* Shap. develops an efficient root architecture that could absorb soil water and nutrition.

2. Materials and methods

2.1. Study site

The Taklamakan desert (337,600 km²) is a leading example of a hyperarid environment (Arndt et al., 2004). The mean annual temperature is 11.9 °C, mean annual potential evaporation is approximately 2600 mm, the mean annual precipitation is only 35 mm and rainfall events are rare and unpredictable (Xia et al., 1993). Ephemeral rivers are fed by snow melt in the Kunlun mountains from spring to autumn. These rivers entering the desert allowed the establishment of river oases along the desert margins. Cele oasis is located at the southern fringe of the Taklamakan desert in Xinjiang Uighur Autonomous Region, NW China. It is on average 10 km in diameter and is surrounded by a 5–10 km belt of sparse vegetation dominated by phreatophytic species (Bruehlheide et al., 2003; Qong et al., 2002). The natural perennial vegetation in the transition zone around Cele Oasis consists of five dominant species; *A. sparsifolia* Shap., *Karelinia caspia*, *Tamarix ramosissima*, *Populus euphratica* and *Phragmites australis* (Bruehlheide et al., 2010).

The study was conducted at Cele National Station of Observation and Research for Desert Grassland Ecosystem (Abbr. Cele Station) near Cele oasis (population 130,000), at 37°00′56.37″N, 80°43′43.81″E, and at an elevation of 1366 m a.s.l. A field site 200 m north of Cele Station at the edge of the desert (37°01′5.66″N, 80°43′47.73″E) was selected for the irrigation study. Groundwater level in the study area was 15 m, and fluctuated little during years. Soil samples were collected throughout the range of depth and soil water content was determined gravimetrically.

2.2. Seed collection

Freshly matured seeds of *A. sparsifolia* Shap. were collected from natural stands at 300 m west of Cele Station in late October 2006. Orbicular seeds were collected after knocking out from the pods with a wood hammer and stored dry in hop-pockets. We measured the viability of seeds with 0.5% triphenyltetrazolium chloride described in detail by Liu et al. (2011) before planting. The germination rate of *A. sparsifolia* Shap. seeds was 93%.

2.3. Study design

Soil water availability was experimentally modified in the study sites through simulated flooding to estimate the contribution of surface water and temporally increased soil moisture to the root

architecture and biomass allocation. We conducted two irrigations and control experiments by establishing and fencing 54 square plots to test the contribution of surface water. Fifty four plots were established throughout a 9720 m² area (81 m×120 m), 6×9 arrangement was used. This study consists of two irrigation levels (0.1 m³/m², 0.2 m³/m²), and a control (0.0 m³/m², CK). Every treatment has 18 plots in a randomized design (Table 1). Each plot was 10 m×10 m, with an interval of 3 m. Soil dams (30 cm height) were made beside each plot to prevent water from effusing between plots. In each case, water covered the entire plot, and the quantity of irrigation water was determined by water meter.

Plants were grown from seeds. Within each plot, 10 seeds were arranged in center. Seeds were sown on the site on 28 March 2007 considering *A. sparsifolia* Shap. in natural stands generally sprout in mid-April both in Cele (Gries et al., 2005) and Washington (Kerr et al., 1965). Each plot was given 0.2 m³ m⁻² irrigation before two days of planting, and the same water was given immediately after planting.

Exclosure was established and fenced to prevent grazing by camel, livestock and small mammals. Dates of irrigation (shown in Table 1) were not uniform due to power failure or lack of workers or sandstorms sometimes. Six plants were randomly selected and totally excavated at the end of growing season from each treatment from 2007 to 2009. Dates of excavation are also given in Table 1.

2.4. Meteorological data

Meteorological variables (Table 2) were recorded by a weather station (Vaisala, M520, Finland) located nearby the study sites. The climate is extremely continental, with cold, dry winters and hot, dry summers.

2.5. Soil samples

Soil was sampled (13 replicates, 13 plots were randomly selected from 54 plots) to monitor initial soil properties (bulk density, organic matter etc.) of the study sites both on irrigated plots as well as on control plots before sowing seeds. Across a vertical soil gradient, soil samples were taken every 20 cm until the maximum depth of the auger was reached (3.4 m). Soil chemical properties (Appendix Table 1) are uniform in the study sites. Silt is the predominant grain size fraction of the soil down to 7.5 m depth, with more than 88% (Bruehlheide et al., 2010). Concentrations of all forms of nitrogen were greater in the upper soil layers and decreased with increasing depth (Appendix Table 1). Soil was sampled (6 replicates) to monitor water content at the end of each growth season from every treatment, and was dried in an oven (105 °C, 48 h). The water content showed in Fig. 2 was the mean value in three years and standard deviation.

Table 1
Study design.

Year	Treatment	Dates of irrigation	Dates of excavation
2007	0 (ck)	–	1 Oct
	0.1 m ³ m ⁻²	1 Apr/2 May/3 Jun/1 Jul/2 Aug/1 Sep	2 Oct
	0.2 m ³ m ⁻²	1 Apr/2 May/3 Jun/1 Jul/2 Aug/1 Sep	3 Oct
2008	0 (ck)	–	1–2 Oct
	0.1 m ³ m ⁻²	2 Apr/1 May/2 Jun/3 Jul/1 Aug/2 Sep	3–4 Oct
	0.2 m ³ m ⁻²	2 Apr/1 May/2 Jun/3 Jul/1 Aug/2 Sep	5–6 Oct
2009	0 (ck)	–	1–2 Oct
	0.1 m ³ m ⁻²	1 Apr/3 May/4 Jun/2 Jul/2 Aug/1 Sep	3–4 Oct
	0.2 m ³ m ⁻²	1 Apr/3 May/4 Jun/2 Jul/2 Aug/1 Sep	5–7 Oct

Table 2
Weather conditions during 3 years measurements.

Factors Year	Precipitation (mm)	Evaporation (mm)	Mean air tempera (°C)	Maximum temperature (°C)	Minimum temperature (°C)	Mean wind speed (m/s)	Prevailing wind direction
2007	40.9	3237.5	14.3	39.6	−13.3	1.33	WNW
2008	40.0	2496.7	13.3	40.1	−24.6	2.0	WNW
2009	59.9	2925.8	14.7	39.2	−23.7	1.43	WNW

2.6. Shoot samples

The number and position of all emerged shoots and sprouts that didn't penetrate surface soil were recorded. At the end of each October, 6 individuals were randomly selected to be harvested. All shoots of target plant were cut at their bases and removed for ease of excavation. The shoots were dried in an oven (75 °C, 48 h), and loaded into envelopes.

2.7. Root samples

Traditional methodology, also referred to as the skeleton method, was used to observe root systems (Bohm, 1979). Trenches, about 1 m wide, were usually dug 3 m away from the base of the target plant and were initially about 10 m long and lengthened as necessary. The investigation was carried out both on irrigated plots as well as on control plots. Root architecture, root biomass and root depth of a

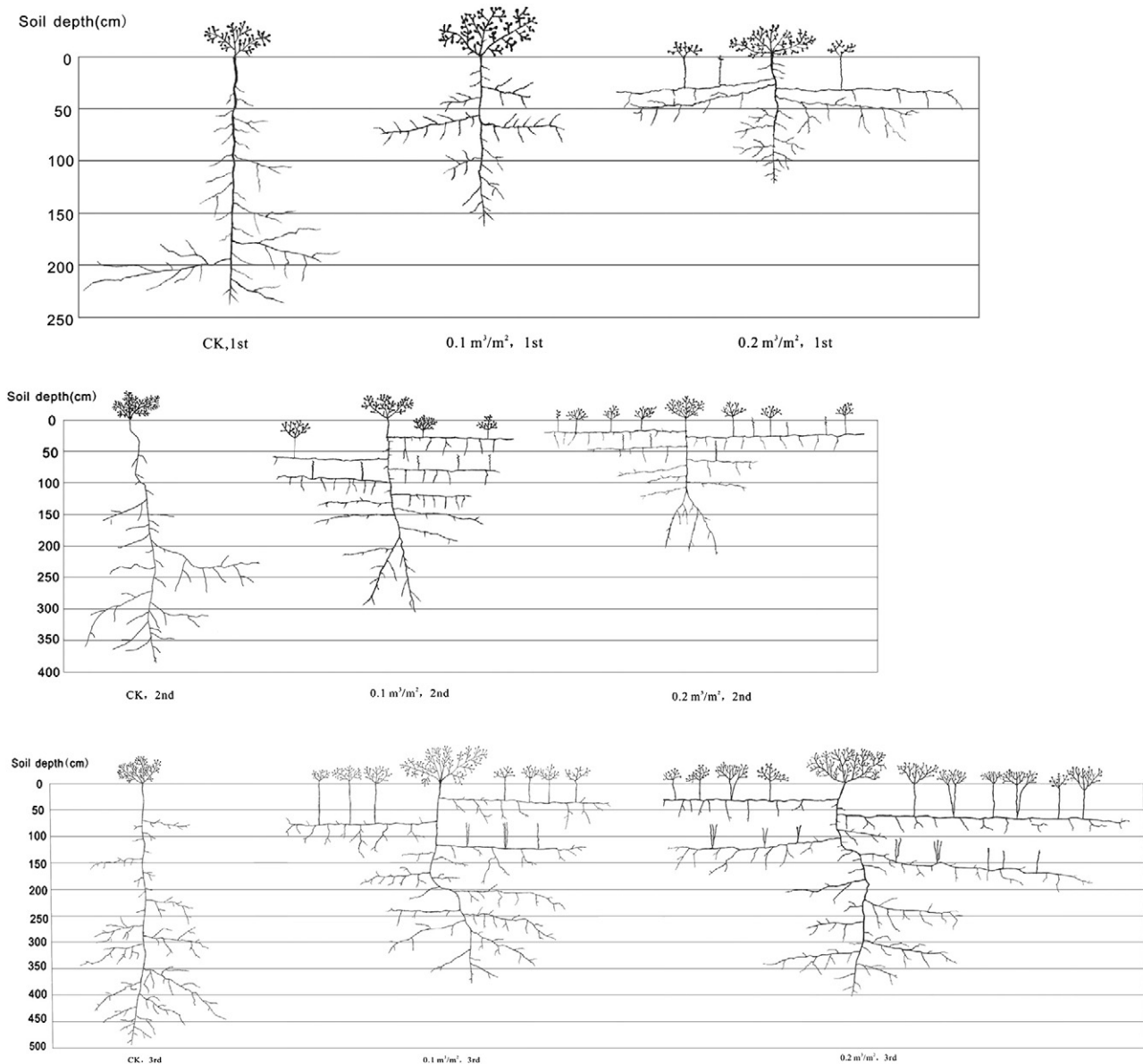


Fig. 1. The roots of *Alhagi sparsifolia* Shap. under different irrigation and age group. Note: Root lengths and depths are drawn to scale, whereas diameters are approximate. CK, 1st means 1 year old with 0 m³/m² irrigation. CK, 2nd means 2 years old with 0 m³/m² irrigation. CK, 3rd means 3 years old with 0 m³/m² irrigation. 0.1 m³/m², 1st means 1 year old with 0.1 m³/m² irrigation. 0.1 m³/m², 2nd means 2 years old with 0.1 m³/m² irrigation. 0.1 m³/m², 3rd means 3 years old with 0.1 m³/m² irrigation. 0.2 m³/m², 1st means 1 year old with 0.2 m³/m² irrigation. 0.2 m³/m², 2nd means 2 years old with 0.2 m³/m² irrigation. 0.2 m³/m², 3rd means 3 years old with 0.2 m³/m² irrigation.

1–3-year-old *A. sparsifolia* Shap. under different irrigation treatments were monitored after root material was excavated in the late fall after growth had been completed in a stratified random fashion with tools in the subsequent three growing seasons. Six different individuals were sampled at each time. Annual and biennial roots of *A. sparsifolia* Shap. were excavated artificially with spades, homemade iron rakes and pickaxes. A pedrail hydraulic excavator was used to dig up profiles around each plot before three-year roots of *A. sparsifolia* Shap. were excavated. The roots were collected every 20 cm of vertical distribution. Large roots were removed from the excavated soil. All major roots (i.e. thicker than 0.5 mm in diameter at their origin or branching points) were traced by careful digging as long as they were visible. The position of branching, termination or bud formation was recorded on a map.

The roots were dried in an oven (75 °C, 48 h). Parameters of root dry biomass, root:shoot ratio, and root depth were determined in an age sequence. Visual assessment was used to separate live and dead roots, dead roots were eliminated in the calculation of the biomass. The roots were carefully separated from the surrounding soil and collected for further measurements. Measurements were made on the day of excavation. The roots were quite fragile and difficult to remove intact. Even with careful hydraulic excavation an unknown fraction of fine roots was inevitably lost, particularly when target roots were tender. Though the excavations failed to recover some unknown proportion of the fine roots that are likely to contribute to root length, we were successful in recovering the majority of the larger roots that contribute most to root biomass.

2.8. Data analyses

Biomass, and soil chemical properties were tested for normal distribution by calculating the Shapiro–Wilk W statistics (SAS version 8.1, The SAS Institute, Cary, NC, USA) for each sets ($n = 6$ for biomass variables, $n = 13$ for soil chemical properties variables). All data were expressed as mean \pm SD. One way ANOVA was used to compare biomass, root:shoot ratio, root depth, and ramet quantity differences in three years. Tukey's test was used to test the differences among treatments when ANOVA showed significant effects ($p < 0.5$).

3. Results

3.1. Root architecture

The root system of *A. sparsifolia* Shap. (Fig. 1) is composed of a taproot, lateral roots, horizontal roots, and adventitious roots. Excavation revealed strong differences among the different irrigation. *A. sparsifolia* Shap. under CK developed tap roots that descended to deeper soil layers, and showed (1) no lateral roots within the top 1 m soil, (2) no living fine root or nodule at the top 0.6 m soil, (3) small lateral fine root branches at deeper soil layers. Adventitious fine roots were detected between 1 m and 2.2 m. *A. sparsifolia* Shap. under 0.1 m³/m² had 16 m long lateral roots and a tap root of only 2 m, and developed a highly branched coarse root system with no distinct tap root. *A. sparsifolia* Shap. under 0.2 m³/m², a total of five new shoots were connected to a single root system (Fig. 1) suggesting ramet production.

The roots of *A. sparsifolia* Shap. under irrigation fall into the specialized prominent lateral type, shoots arise from the laterals, the tap roots penetrate to a depth of 450 cm. *A. sparsifolia* Shap. grows new entire shoots each season, and no fine roots were detected in the dry soil profile (Fig. 2). Shoot from the root system occurs in the first growing season (0.2 m³/m²). *A. sparsifolia* Shap. grown in the plots had extended its territories producing new shoots through ramets that grow on horizontal coarse root (usually with diameter more than 0.7 mm). The root system consisted of clearly distinguishable horizontal and vertical roots, and extended approximately 1.5–2 m in

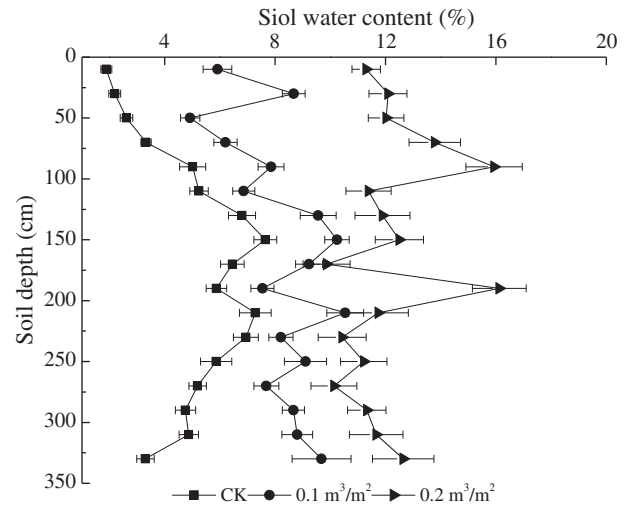


Fig. 2. Soil water content (Mean \pm SD).

radius and 120 cm in depth at least. Horizontal roots were typically 6–20 mm in diameter, emerging radially from the tap root and creeping at a depth of 30–100 cm. The vertical tap roots were 6–25 mm in diameter, and penetrated depths were from 160 cm to 450 cm (Fig. 1).

3.2. Total biomass, root:shoot ratio and root depth

The plants growing on irrigation (0.1 m³/m², 0.2 m³/m²) were more vigorous than those control (Table 3). The total number of root branches, seed yields and total root system length was greater after irrigation and with an increase in shoot dry weight. Total biomass decreased with decreasing irrigation but below-ground biomass decreased at a slower rate than above-ground biomass. During less irrigation, the root/shoot ratio was higher, particularly in October at the end of the growing season. *A. sparsifolia* Shap. distributed more biomass to roots under drought conditions. Thus, plant may regulate their root/shoot ratio to adapt to drought and water stress. The seedlings distributed biomass mainly to shoots early in the first growing season to capture more light and other resources, but distributed more biomass to roots for reserves in the next two growing seasons.

3.3. Root biomass of different depth and cumulate biomass

Root biomass of different depths (Fig. 3) showed an 'inverted pyramid-shape' in vertical section view under different irrigation treatments. The root biomass decreased gradually with increased soil depth. Root biomass of *A. sparsifolia* Shap. reaches maximum within depths of 20–40 cm in the CK treatment, and declined gradually in deeper soil. In irrigation treatments, the root biomass reached maximum value at depths 0–20 cm and roots were mainly concentrated in soils with depths of <80 cm, root biomass was concentrated in the surface for excellent moisture conditions, irrigation promoted root biomass accumulation, while irrigation militated against root growth depth.

4. Discussion

We have limited understanding of architecture and biomass of root systems in hyperarid environment. Flood irrigation had little beneficial effect on nitrogen metabolism and growth of *A. sparsifolia* Shap. (Arndt et al., 2004; Zeng et al., 2006; Thomas et al., 2006). Studies on longer-term effects of flood irrigation in the study area revealed that the additional surface water still had little influence on water status and leaf water use of the studied species (Foetzi, 2004; Thomas,

Table 3
Biomass.

Treatment	Biomass				Root:shoot ratio	Root depth	Ramet no.	
	Leaf	Stem	Root	Seed				
One year old	ck	1.51 ± 0.31d	1.97 ± 0.35e	13.00 ± 1.11e	0	3.83 ± 0.73c	2.32 ± 0.06d	0
	0.1	2.52 ± 0.34d	3.78 ± 0.37e	17.70 ± 1.61e	0	2.82 ± 0.27d	1.71 ± 0.05e	0
	0.2	4.85 ± 0.83d	7.67 ± 0.89e	28.11 ± 1.18e	0	2.27 ± 0.21d	1.28 ± 0.05f	2.2d
Two years old	CK	1.40 ± 0.21d	3.25 ± 0.43e	31.70 ± 1.77e	0	6.84 ± 0.54b	3.91 ± 0.05b	0
	0.1	23.7 ± 7.22c	47.69 ± 11.38d	182.38 ± 10.56d	0	2.64 ± 0.47d	2.89 ± 0.06c	3.1c
	0.2	39.33 ± 7.35b	80.30 ± 9.11c	265.09 ± 18.65c	2.18 ± 0.27b	2.19 ± 0.18d	2.28 ± 0.05d	6.9b
Three years old	CK	1.62 ± 0.24d	3.64 ± 0.58e	46.41 ± 3.35e	0	9.01 ± 1.75a	4.51 ± 0.04a	0
	0.1	79.98 ± 18.22a	166.94 ± 27.88b	567.96 ± 90.78b	1.51 ± 0.24c	2.29 ± 0.17d	3.92 ± 0.07b	7.4b
	0.2	89.64 ± 27.35a	195.30 ± 43.72a	645.39 ± 144.89a	5.04 ± 0.48a	2.24 ± 0.31d	3.90 ± 0.06b	10.8a

Values are means ± SD. Letters indicate significant differences between years for each date (Scheffe test, n = 6). $P < 0.5$.

2004; Gries et al., 2005). But in our study, longer-term irrigation had significant influence on root biomass, the quantity of ramet, and the root architecture between the irrigated and the non-irrigated plots.

For the first year growth was apparently normal, and the controls were far behind those treated with irrigation, yet they seemed to be healthy. But when the rest of the series were beginning to the third year the CK plants presented a very abnormal appearance. They were small, stunted, and dark green in color, while none of the plants bloomed.

Excavations have shown a great quantity of horizontal roots of *A. sparsifolia* Shap. buried between 10 cm and 100 cm depth. Horizontal roots produced shoots but the vertical roots did not, suggesting that the latter may primarily serve as a storage and propagation organ. A large number of ramets sprout from coarse horizontal roots that provide an opportunity for vegetative restoration. In our excavation carried in 2011 in natural stands, horizontal roots produced three shoots even under 470 cm (unpublished data). However, the vertical roots are also capable of producing shoots at the surface soil (unpublished data).

Fine roots are important in the acquisition of water and essential nutrients (Pregitzer, 2008). Excavations of surface roots and soil sampling did not reveal any fine roots in the top dry soil profile of CK treatment. This result was confirmed in numerous excavations at other study sites in this area (Arndt et al., 2004) and soil coring using an auger (Thomas et al., 2000) in natural stands. In this respect the root system structure of *A. sparsifolia* Shap. is very different from that of forests that rely on rain for their water supply or of orchard trees that are regularly irrigated.

Root system architecture is greatly influenced by the soil availability and distribution of nutrients (Kochian, 2012). Soil nutrient concentration (e.g. organic carbon, total nitrogen, available nitrogen, etc.) in study site is very low and the spatial distribution of mineral nutrients is highly homogeneous (Appendix Table 1). Low phosphate availability may favor lateral (Williamson et al., 2001). *A. sparsifolia* Shap. develops dichotomous root systems, that contribute to the potential competitiveness of plants growing in nutrient limited soil.

Grasses develop a dense and shallow root system (Muñoz-Romero et al., 2010). But in our study, the root system of *A. sparsifolia* Shap.

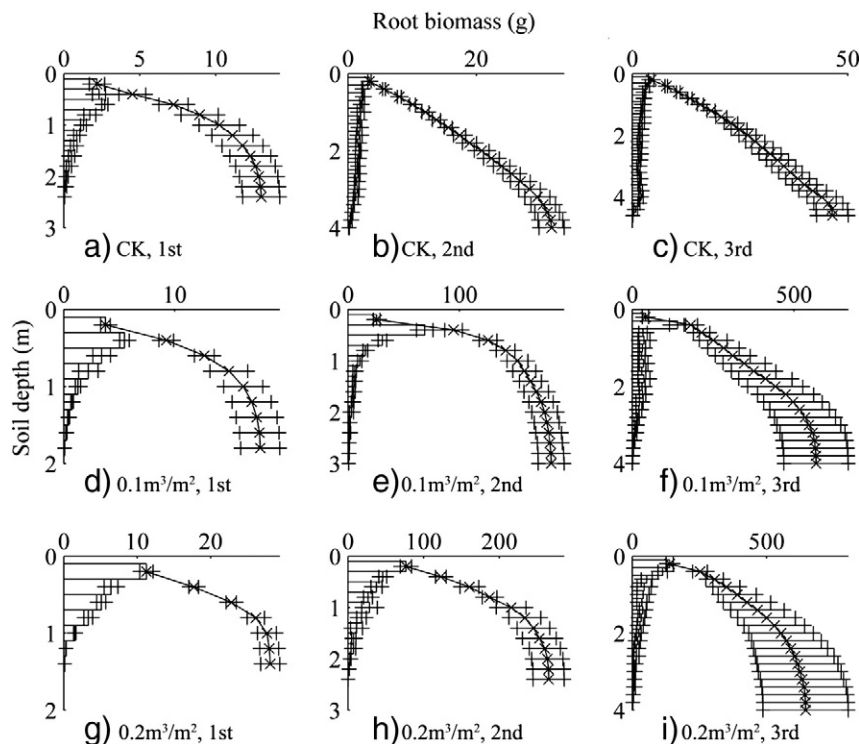


Fig. 3. Root biomass of different soil depth and cumulate biomass. Note: The means of every abbreviation is the same as Fig. 1.

can be very deep. The root system of 3 year old *A. sparsifolia* Shap. can even reach 4 m under a good water availability. The lack of rainfall events and soil moisture in the CK plots precludes nutrition uptake from soil and root excavations revealed only negligible amounts of live roots in the upper soil layers. Early in the treatment processing, there were some fine roots, but subsequently rainfall events in this region had no contribution to their water supply (Gries et al., 2005), they died due to lack of sustained water supply (Arndt et al., 2004; Thomas et al., 2000) before the first excavation. The soil water potential of top 10 cm depth was -61.48 Mpa on 8 August 2008 (WP4-T, Decagon, USA; soil water was 0.61%). The lack of fine root growth is consistent with evidence that fine roots are often unable to survive in soils with very negative water potentials (Nobel, 1994). This is not surprising given the climatic regime at this site (Zeng et al., 2006).

Plants can survive for three years after twice irrigation in CK, because *A. sparsifolia* Shap. is a fast-growing species, whose total above-ground biomass is formed within 56 days (Rzepecki et al., 2011) in natural stands. Another factor that may contribute to an effect of twice irrigation accumulated water in the soil profile. Silt is the predominant particle size fraction so the soil has excellent water

storage capacity, and low infiltration and transport rates (Gries et al., 2005; Bruelheide et al., 2010), this is sought to be another positive factor. It was hypothesized that successful survival of *A. sparsifolia* Shap. depended on root systems with an architecture which could exploit soil resources, particularly soil water. The importance of root system biomass, particularly to modelers of global carbon balance (Jackson et al., 1996) is recognized but is not addressed. From our data we conclude that the phreatophytic perennial species investigated have adapted to the hyperarid environmental conditions through rapid development of root systems to satisfy demands for both water and nutrients. We agree with the view that was proposed by Vonlanthen et al. (2010).

Acknowledgments

This work was supported by the Knowledge Innovation Program of the Chinese Academy of Sciences (KZCX2-EW-316) and the National Natural Science Foundation of China (U1203201, 31100144, 31070477, 30870471).

Appendix A

Appendix Table 1

Soil nutrition concentration.

Depth (cm)	Organic carbon (g/kg)	Total nitrogen (g/kg)	Total phosphorous (g/kg)	Total potassium (g/kg)	Available nitrogen (mg/kg)	Available phosphorous (mg/kg)	Available potassium (mg/kg)	Bulk density (g/cm ³)
0–20	0.481 ± 0.147	0.023 ± 0.007	0.066 ± 0.008	1.78 ± 0.10	28.16 ± 16.14	11.83 ± 7.49	184.5 ± 124.7	1.35 ± 0.01
20–40	0.333 ± 0.130	0.016 ± 0.007	0.061 ± 0.006	1.77 ± 0.12	18.21 ± 9.70	6.65 ± 4.48	173.7 ± 122.6	1.37 ± 0.02
40–60	0.235 ± 0.063	0.012 ± 0.003	0.064 ± 0.004	1.74 ± 0.10	11.60 ± 5.94	4.11 ± 2.48	181.4 ± 138.4	1.43 ± 0.02
60–80	0.233 ± 0.056	0.011 ± 0.002	0.057 ± 0.004	1.79 ± 0.11	8.43 ± 2.75	3.93 ± 2.59	180.1 ± 153.5	1.45 ± 0.01
80–100	0.211 ± 0.040	0.011 ± 0.003	0.058 ± 0.003	1.76 ± 0.08	7.65 ± 2.98	3.39 ± 2.14	171.0 ± 139.8	1.41 ± 0.02
100–120	0.209 ± 0.023	0.010 ± 0.001	0.057 ± 0.005	1.77 ± 0.08	7.98 ± 3.32	2.66 ± 1.78	168.5 ± 137.8	1.42 ± 0.02
120–140	0.231 ± 0.057	0.012 ± 0.004	0.056 ± 0.004	1.79 ± 0.08	8.43 ± 4.16	2.24 ± 1.26	169.8 ± 137.5	1.39 ± 0.06
140–160	0.244 ± 0.032	0.012 ± 0.002	0.055 ± 0.006	1.82 ± 0.13	7.96 ± 4.47	1.35 ± 0.79	172.5 ± 139.6	1.41 ± 0.02
160–180	0.236 ± 0.066	0.011 ± 0.003	0.057 ± 0.005	1.80 ± 0.13	8.57 ± 4.97	0.97 ± 0.43	166.6 ± 134.3	1.39 ± 0.04
180–200	0.193 ± 0.037	0.010 ± 0.003	0.058 ± 0.005	1.76 ± 0.10	6.62 ± 3.68	1.97 ± 0.44	174.0 ± 149.8	1.36 ± 0.06
200–220	0.210 ± 0.028	0.011 ± 0.003	0.055 ± 0.007	1.82 ± 0.08	6.75 ± 4.33	1.16 ± 0.40	172.7 ± 147.0	1.36 ± 0.03
220–240	0.230 ± 0.038	0.012 ± 0.003	0.058 ± 0.003	1.82 ± 0.09	7.65 ± 5.59	0.89 ± 3.06	179.6 ± 155.2	1.35 ± 0.08
240–260	0.264 ± 0.068	0.013 ± 0.004	0.058 ± 0.003	1.85 ± 0.09	9.00 ± 6.52	1.45 ± 0.87	192.2 ± 181.6	1.36 ± 0.02
260–280	0.229 ± 0.046	0.011 ± 0.002	0.060 ± 0.009	1.81 ± 0.10	9.41 ± 8.07	1.06 ± 0.51	170.7 ± 157.6	1.35 ± 0.03
280–300	0.203 ± 0.038	0.011 ± 0.003	0.060 ± 0.004	1.84 ± 0.08	8.72 ± 6.47	1.00 ± 0.44	147.9 ± 122.5	1.37 ± 0.03
300–320	0.192 ± 0.040	0.010 ± 0.002	0.061 ± 0.010	1.81 ± 0.11	7.40 ± 3.69	0.93 ± 0.27	134.3 ± 108.2	1.32 ± 0.03
320–340	0.190 ± 0.059	0.009 ± 0.003	0.061 ± 0.008	1.78 ± 0.12	9.18 ± 4.49	0.97 ± 0.50	127.4 ± 90.6	1.34 ± 0.01

Values are means ± SD.

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