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Root biomass distribution of planted *Haloxylon ammodendron* in a duplex soil in an oasis: desert boundary area

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Abstract Duplex soils, consisting of a sandy surface soil (A-horizon) and silty-clay subsoil (B-horizon), occur in a boundary area between oasis and desert in northwestern China and create a challenging habitat for restoration of plant growth. We conducted an experiment in a 10-yearold *H. ammodendron* plantation forest to determine the influence of physical properties of duplex soil on water infiltration and plant root growth. We used a trenching method to assess root biomass, and classified roots into two diameter classes: fine (<2 mm) and coarse (>2 mm). Following a 26.7 mm rain event, water infiltrated to the B- horizon; further deep percolation was hindered by low hydraulic conductivity, so that B horizon remained at high available soil moisture for an extended period of time. Root biomass increased rapidly in, or very close to the B horizon, especially for coarse roots. The subsoil formed a barrier to root penetration, but may also reflect the accumulation of water resources at the boundary between the A- and B-horizon. Shoot growth and root distribution, shrub height and canopy area, and total root biomass were negatively correlation with depth to the B horizon, and that was reflected by quadratic functions. We conclude that the texture and structure of duplex soils influenced the soil environment for water infiltration and storage, indicating that the B-horizon underlying sand in duplex soils is advantageous for the growth, and development of planted sandstabilizing vegetation. These results have important implications for sustainable development of sand-fixing plantations in desert ecosystems.

Keywords Soil texture · Soil properties · Root biomass and distribution · Water infiltration · Water storage

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Introduction

Desertification is a land-degradation process caused by intensification of human activities and climate change in fragile ecosystems of arid and semi-arid areas, and constitutes a major threat to the sustainability of agriculture and economic development (Zhu and Liu 1988; Lal 2000; Wang 2000). Preventive measures have been developed and successfully implemented in China, and include the use of wheat-straw, and planting of indigenous dune-adapted shrubs to curb desertification and alleviate its influence on crops, pasture, and human life (Zhang et al. 2004; Li et al. 2009; Liu et al. 2013). Further, once a population of indigenous shrubs is established, it can accrue more resources, either actively through root uptake of soil water and nutrients, or passively by accumulating wind-blown dust and litter (Garner and Steinberger 1989; Gutiérrez et al. 1993; Burke et al. 1995): this accrual creates a feedback mechanism that facilitates invasion and colonization by other plant species (Li et al. 2009). However, the survival of planted dune-adapted shrubs is affected by the properties of species and microhabitats (Reynolds et al. 1999; Wijesinghe and Hutchings 1999; Ren et al. 2002). Many studies have demonstrated that Haloxylon ammodendron is the preferred sand-stabilizing species because of its resistance to drought, cold, salt-alkali, and poor soil quality (Tobe et al. 2000; Ma et al. 2007), and its ability to alter the root system to maintain function and growth with limited soil resources (Bell and Sultan 1999; Xu et al. 2007; Xu and Li 2008).

The relationship between water availability of desert shrubs and their individual morphology, especially foliage growth and root-system distribution, is critical for the survival of these plants (Xu et al. 2007). Individual shrubs can adjust their morphology to maximize resource acquisition and escape or endure biotic and abiotic stresses (Weijschede et al. 2006; Messier et al. 2009). For plants experiencing water-limited conditions, the ability to alter root systems is important for enduring

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water stress and acclimating to changing habitat conditions (Bell and Sultan 1999; Schenk and Jackson 2002; Xu and Li. 2008). Water availability and, consequently, root distribution, depend strongly on soil physical properties throughout the soil profile—texture, porosity, and hydraulic conductivity (Fravolini et al. 2005; Macinnis-Ng et al. 2010).

Sudmeyer et al. (2004) suggested that root density generally decreased with increasing depth. However, this decrease was relatively gradual in deep sands, and abrupt in clay subsoils, because dense subsoil clays form a barrier to root growth. The decrease in root density may also reflect the accumulation of water and nutrients at the boundary between sand and clay (Laclau et al. 2001; Sudmeyer et al. 2004). Sandy soils are generally associated with higher porosity and hydraulic conductivity than fine-textured soils, and may offer less resistance to root penetration, thus facilitating root elongation (Saxton and Rawls 2006). Additionally, strong differences in texture between surface and subsurface soil horizons have significant effects on soil hydrology and on conditions for plant growth (Chittleborough 1992). Studies of the mechanisms of water movement in layered soil profiles suggest that the depth of each layer relative to the total profile depth can have an overriding effect on water entry, storage, and movement (Tennant et al. 1992). Examples of predicted behavior given by Hillel and Talpaz (1977) for 17 uniform and layered profiles show high storage efficiencies in duplex soils, in which the subsoil (B horizon) is at least one-and-a-half texture-groups finer than the surface soil (A horizon) (Chittleborough 1992; Tennant et al. 1992). The sandysurfaced A horizons have higher infiltration rates and lower evaporation losses than the B horizons.

In most ecosystems, roots tend to be most abundant in topsoil layers, decreasing exponentially with increasing soil depth (Schenk 2008). Xu and Li (2008) investigated root distribution of Haloxylon ammodendron in uniform coarsetextured and loamy-textured soil profiles and showed that plants in sandy soil developed much deeper root systems and larger root surface areas than in loamy-textured soil, which indicated that plants have an advantage of growth in coarse-textured soil. However, plant shoot size and root distribution in a duplex (texture contrast) soil have not been investigated, especially in a sand-fixing forest. The objectives of this study were to: (1) quantify root biomass in a duplex soil with a variable depth of the surface sand layer; (2) determine the optimal combination of soil A and B horizons which ensures plant survival and individual development in desert-oasis landscapes.

Materials and methods

Study site and experimental design

The study was conducted in 2014 (June to September) in an *H. ammodendron* forest planted in a desert–oasis ecotone at the southern edge of the Badain Jaran Desert in northwestern China. The area is located near the Linze Inland River Basin Research Stations of the Chinese Academy of Sciences (CAS) (39°21'N, 100°07'E). The area has a continental arid temperate climate, with hot, dry summers, and cold winters. Mean annual temperature is 7.6 °C. Mean annual precipitation is 116.8 mm (1965–2000), and over 80 % of the precipitation occurs between May and September. Mean annual open water evaporation is 2390 mm.

The study site is located at the elevation of 1,374 m a.s.l. Prior to planting of sand-fixing vegetation, the site was characterized by moving sand dunes alternating with lightly undulating interdunal lowlands. Soils are sandy, very loose in structure, and highly susceptible to wind erosion. The surface sand deposits are 30–500 cm deep; the subsoil contains a clay pan (Shen et al. 2014). Thus, soils consist of a duplex profile with substantially differing physical properties between the surface and the subsoil. Rainfall data are collected by the Automatic Weather Observing System (HOBO, USA) at the Linze Inland River Basin Research Stations of the Chinese Academy of Sciences.

Haloxylon ammodendron was manually planted in 2004 using single-stems in rows at about 2.0 m \times 2.5 m spacing. Twelve 10 m \times 10 m sampling plots were established in this plantation forest. We measured the thickness of surface sand (A horizon) with a soil auger, and found that it ranged from 30 to 200 cm (Table 1). We used a caliper to measure plant height, canopy radius, and basal diameter in each plot. We determined the maximum rooting depth with the trenching method (details in next paragraph). We also counted the number of individuals in three quadrats (10 m \times 10 m).

Soil physical characteristics

In each sampling plot, six transects perpendicular to the tree row (one side only, side selected randomly) were marked. Then, two adjacent trenches were constructed between two trees (Fig. 1). The trenches were about 1 m wide (parallel to the tree row at a distance of 10 cm) \times $1 \text{ m long} \times 2 \text{ m deep.}$ Three replicate soil samples (1000 cm^3) were collected at 10 cm intervals to 2 m depth along one wall of each trench using metal corers (10 cm in diameter); soil samples were then transported to the laboratory in air-tight plastic bags. One set of samples from each plot was oven dried at 105 °C for 48 h to determine bulk density, expressed as dry mass divided by the soil volume (g cm⁻³) (Macinnis-Ng et al. 2010). Another set of samples was used to measure soil particle sizes by wet-sieving and hydrometer methods (Arthur et al. 2012). Saturated soil hydraulic conductivity was measured using a constant head method (Reynolds and Elrick 2002) in intact cores from the twelve plots. Soil water potentials were measured with WP4-T Dewpoint PotentiaMeter (Decagon Devices, Pullman, WA) (Lu et al. 2008). Then subsamples of each soil were adjusted to relative water content (RWC) that

Table 1 Canopy structure and tree morphology of trees in the 12 sampling plots

Plot no.	Tree height (cm)	Canopy area (cm ²)	Basal diameter (cm)	Tree spacing (cm)	Root depth (cm)	Depth of sandy surface layer (cm)
1	141.6	8655.3	2.16	200	265.4	200
2	134.5	10132.3	2.65	210	258.6	200
3	116.2	6050.6	2.22	200	253.5	180
4	189.5	11788.2	3.48	200	232.3	170
5	157.7	10841.6	2.67	200	208.7	140
6	171.1	10818.2	3.04	200	195.7	120
7	149.8	17629.5	2.79	200	187.2	120
8	249.3	18734.3	4.44	220	175.9	80
9	202.9	12375.4	3.60	190	183.1	80
10	230.3	17566.7	4.38	200	164.3	70
11	191.2	15762.2	3.33	220	169.2	60
12	254.7	17006.1	4.10	235	158.4	30

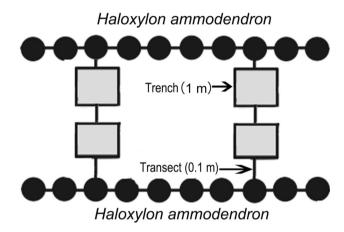


Fig. 1 Soil and root sampling positions in a planted *Haloxylon* animodendron forest. Black dots show positions of *Haloxylon* animodendron trees

coincided with water potentials ranging from -0.06 to -1.46 MPa. We subsequently multiplied RWC by bulk density to get volumetric water content (VWC) values. Soil water retention curves were determined with RETC version 6.0 and van Genuchten's equation (van Genuchten 1980; Macinnis-Ng et al. 2010):

$$S_e = \frac{1}{\left[1 + \left(ah\right)^n\right]^m}$$

where S_e is the effective degree of saturation, h is suction (cm) and α , n and m are empirical constants affecting the shape of the retention curve.

In each plot, we measured soil water content (see below) on the 15th day of each month from June to September. We also compared data from before a rainfall event on the 15th of July with those measured on the 23rd and the 27th of July (a 26.7-mm rainfall occurred on the 22nd of July). Soil samples were collected by hand auger from 0 to 200 cm depth. The samples between 0–100 cm depth were obtained at 10-cm intervals, and those between 100 and 200 cm depth were obtained at 20-cm intervals. Three repli-

cates for each depth interval were obtained from three independent cores in each plot for a total of 9 samples per depth interval per plot. Soil water content (mass ratio) was obtained by a conventional oven-drying method.

Root biomass distribution

We used the trenching method (Komiyama et al. 1987) to investigate root biomass and distribution. Six trenches were made in each sampling plot in early August, as described above (two trenches per quadrat, three quadrats per plot). Soil samples were collected from each soil layer at 10 cm intervals to 2 m depth in each trench. These samples were transported to laboratory in plastic bags. Roots were separated from the soil by washing through a 0.5-mm sieve, and sorting into coarse (>2 mm diameter) and fine (<2 mm diameter) fractions. Roots with diameters of <2 mm were generally defined as feeder roots for water and mineral uptake (Gordon and Jackson 2000; Wang et al. 2015). Roots were then stored in paper bags until oven-drying at 60 °C for 48 h to a constant weight.

Root biomass was expressed on a ground-area basis (kg m^{-2}) and as root density (root mass expressed on a soil-volume basis, kg m⁻³) (Eamus et al. 2002).

Data analyses

All statistical analyses were conducted with SPSS software (version 17.0, SPSS Inc. Chicago, IL, USA). After performing one-way ANOVA, the LSD test for multiple comparisons was used to detect differences among plots in plant total root biomass with depth of A horizons. Significance was determined at the 95 % confidence level (a = 0.05). The Pearson Correlation Coefficient was used to explore relationships between tree root biomass, canopy area, tree height, rooting depth, and soil properties at 0–2.0 m depth. The relationships between depth of sand (surface soil), maximum rooting depth, and tree height were described with a quadratic function.

 Table 2 Measured soil texture and soil water characteristics of the A and B horizons

Variable	A-horizon (mean ± SE)	B-horizon (mean ± SE)
Sand component (%)	89.52 ± 0.54	11.12 ± 1.32
Silt component (%)	5.97 ± 0.23	57.80 ± 0.38
Clay component (%)	4.51 ± 0.54	31.08 ± 1.86
Bulk density (g cm $^{-3}$)	1.46 ± 0.02	1.33 ± 0.027
Saturated hydraulic	$2.52~\pm~0.04$	0.01 ± 0.004
conductivity K_s (mm min ⁻¹) Saturated soil moisture	$26.20~\pm~0.69$	39.77 ± 1.16
content $\theta_{\rm s}$ (%)	26.02 + 0.50	50.02 L 2.02
Capillary porosity (%) Total porosity (%)	$\begin{array}{r} 36.92 \ \pm \ 0.59 \\ 38.14 \ \pm \ 0.48 \end{array}$	$\begin{array}{r} 50.82 \ \pm \ 2.82 \\ 53.12 \ \pm \ 2.09 \end{array}$

Results

Soil physical characteristics

Soils at our study site had two different layers of contrasting texture; such soils are defined as duplex soils in which basic soil properties differ substantially between lavers. Thus, texture of the surface soil was coarse sand, while that of subsoil was heavy clay. The boundary between the surface soil and subsoil was distinctive, and the change from surface to subsoil texture occurred over a depth of 10 cm or less (Table 2). Surface soil, or the A-horizon, was composed of sandy soil with about 89.52 % sand, 5.97 % silt, and 4.51 % clay. This layer had a mean bulk density of 1.46 \pm 0.02 g cm⁻³, saturated hydraulic conductivity soil (K_s) of $2.52 \pm 0.04 \text{ mm min}^{-1}$, saturated soil moisture content (θ_s) of 26.20 \pm 0.69 %, capillary porosity of 36.92 \pm 0.59 %, and total porosity of 38.14 ± 0.48 %. The subsoil, or the B horizon, had a higher silt (at 57.80 %), clay (at 31.08 %), and θ_{s} (at 39.77 \pm 1.16 %), but lower bulk density (at $1.33 \pm 0.027 \text{ g cm}^{-3}$) and K. $(0.01 \pm 0.004 \text{ mm min}^{-1})$ than the A-horizon. The differences in soil water retention curves between the A and B horizons were attributed primarily to the differences in pore-size distribution (Fig. 2). These curves are sensitive to disturbance of soil structure. Sandy soils involved mainly capillary binding, and therefore released most of the water at higher potentials, while clayey soils, with adhesive and osmotic binding, released water at lower (more negative) potentials.

Precipitation and soil water content

Precipitation was unevenly distributed through time at our study site. Over 80 % of precipitation in 2014 occurred between May and September (Fig. 3). Precipitation events of 5 mm or less accounted for 44.07 % of total annual precipitation and 86 % of the events. Events of 5–10 mm comprised 24.83 % of annual pre-

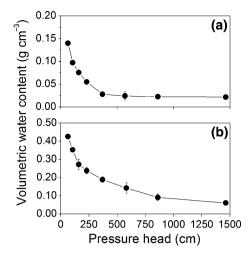


Fig. 2 Soil water retention curves for the A- (a) and B- (b) horizons. *Curves* were fitted using the van Genuchten model. *Error bars* represent standard errors of mean soil volumetric water content, n = 3

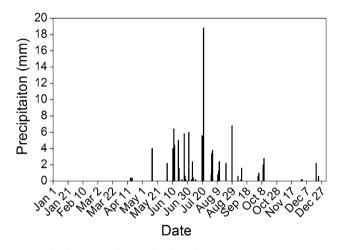
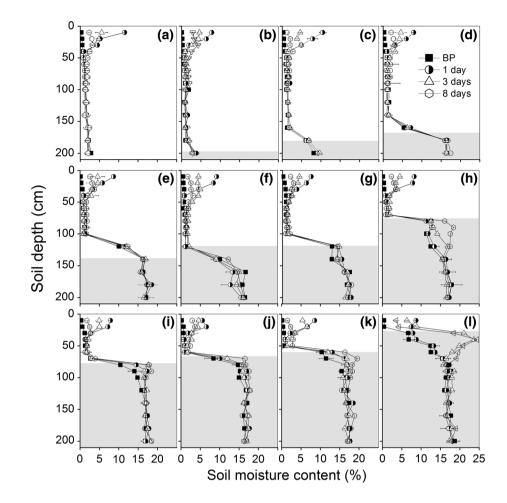


Fig. 3 Distribution of precipitation during 2014 in an oasis and desert boundary area, northwestern China

cipitation and 8.79 % of the events. Events >15 mm were sparse. The largest precipitation was 26.7 mm and fell on 21st to 23rd of July, 2014.

The typical pattern of soil moisture in the duplex soil profile following rainfall is displayed in Fig. 4. Before precipitation, soil water content increased slightly with depth in the A-horizon, and rapidly in the B-horizon. After a large precipitation event (26.7 mm), soil moisture increased significantly (F = 11.34, P < 0.01), and rain water infiltrated quickly into the sandy layer. However, soil water content increased more in the upper profile in the duplex soils than in the uniformly-sandy soil at the same depth, especially in plots where the depth of the A- horizon was < 80 cm (Fig. 4). The silty-clay layer hindered water infiltration due to its low saturated soil hydraulic conductivity (K_s), and remained at high soil moisture content for an extended period of time.

Fig. 4 Soil water content in the profile containing A- and B-horizons (*gray shading*) before and after 26.7 mm of precipitation on July 23rd in each plot. BP means before precipitation. Panels **a**, **b** represent plots 1-12. *Error bars* represent standard errors of mean soil moisture content, n = 3



Root biomass distribution

Root biomass differed significantly among the sampling plots with different depths to the B horizon (F = 24.32, P < 0.01). For plots where depth to B horizon was > 1.5 m (No. 1, 2, 3, 4), total root biomass was about 0.60 kg m⁻² with 50 % of the roots being coarse. However, at two other plots (11, 12), where depth to B horizon was < 1.0 m, total root biomass was > 2.0 kg m⁻² with about 80 % of the roots being coarse (Table 3). In a uniform sandy soil profile (plots 1, 2) roots penetrated to > 2.0 m below the soil surface (Fig. 5a, b), but at plots 11, and 12, where depth of the sandy layer was < 0.5 m, roots reached only 1.5 m (Fig. 5j, k, l).

Distribution of root biomass differed significantly with soil depths (Fig. 5). Root biomass was very low in the top 20 cm, and accounted for < 8 % of the respective totals. Most roots were concentrated at depths between 0.5 and 1.0 m, which accounted for more than 60 % of total root biomass in plot 1 and 7, where the soil profile was uniformly sandy (Fig. 5a, b). The distribution of root biomass also reflected the duplex nature of the soil profile which changed the traditional distribution of root biomass in that biomass increased abruptly in the silty-clay layer, especially for coarse roots (Fig. 5). This also led to a bimodal root distribution in both—top 0.5 and in 1.5 m of the duplex soil profile at plots 6, 7 and 9, where depth to the B-horizon was about 1.0 m. Coarse root biomass in the B-horizon was several magnitudes greater than that in the A-horizon in all plots except one, where depth of the sandy layer was > 1.5 m. The proportion of coarse root biomass was <20 % in the A-horizon, but > 80 % in the B-horizon. Fine root biomass was similar across plots in the sandy layer, but increased in the silty-clay layer. Fine root biomass increased with depth in the top soil, but declined in the subsoil, although the quantities were different between the sites (Fig. 5). The proportion of fine root biomass was about 45 % in the A-horizon and about 20 % in the B-horizon.

Plant growth in duplex soil

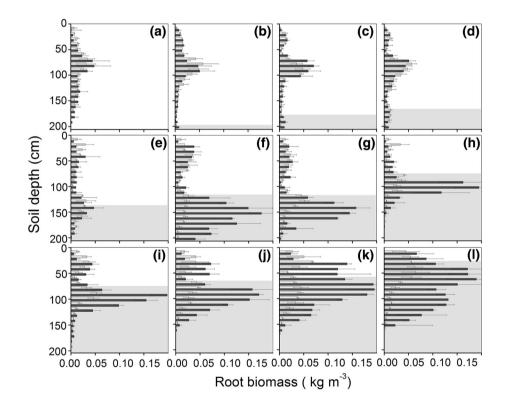
Most of the tree-growth characteristics were significantly correlated with soil properties in this study (Table 4). Total root biomass (in the 0–2 m soil depth) was positively correlated with clay, and negatively with sand content, Ks, and depth to the B-horizon. Fine root biomass was generally poorly correlated with soil properties (Table 4). Tree height and canopy area were

Table 3 Root biomass (mean \pm SE) per plot

Plot no.	Total root biomass (kg m ⁻²)	Fine root biomass (kg m ⁻²)	Coarse root biomass (kg m ⁻²)	Coarse roots/total roots ratio (%)
1	0.59 ± 0.13^{a}	$0.28 \pm 0.09^{\rm a}$	0.31 ± 0.18^{a}	52.98
2	$0.62 \pm 0.03^{\rm a}$	0.33 ± 0.01^{a}	$0.29 \pm 0.04^{\rm a}$	47.13
3	$0.75~\pm~0.05^{ m ab}$	$0.37 \pm 0.06^{\rm a}$	$0.37~\pm~0.05^{ m ab}$	50.00
4	0.63 ± 0.01^{ab}	$0.31 \pm 0.09^{\rm a}$	0.32 ± 0.12^{ab}	50.32
5	0.60 ± 0.14^{ab}	$0.29 \pm 0.10^{\rm a}$	0.32 ± 0.18^{ab}	52.44
6	$1.51 \pm 0.20^{\rm b}$	0.35 ± 0.10^{ab}	1.16 ± 0.31^{b}	76.84
7	1.33 ± 0.29^{b}	0.34 ± 0.10^{ab}	$0.99 \pm 0.48^{\rm b}$	74.67
8	$0.89 \pm 0.15^{\rm b}$	0.24 ± 0.08^{ab}	$0.65 \pm 0.23^{\rm bc}$	73.15
9	$1.11 \pm 0.14^{\rm bc}$	0.33 ± 0.09^{ab}	$0.78 \pm 0.19^{\rm bc}$	70.07
10	$1.43 \pm 0.19^{\rm bc}$	$0.37 \pm 0.13^{\rm ab}$	$1.05 \pm 0.26^{\circ}$	73.80
11	$2.00 \pm 0.25^{\circ}$	$0.48 \pm 0.13^{\rm b}$	$1.53 \pm 0.36^{\rm cd}$	76.24
12	$2.15 \pm 0.53^{\circ}$	$0.46 \pm 0.14^{\rm b}$	$1.69 \pm 0.93^{\rm cd}$	78.56
F	93.32	14.38	111.41	
Р	< 0.001	< 0.001	< 0.001	

Different lowercase letters (a, b, c, d) within root type indicate significant differences among plots

Fig. 5 Distribution of fine (gray bar) and coarse (dark bar) root biomass through the soil profile in 12 plots. The gray-shaded area represents the B-horizon. **a**, **b** represent plots 1-12. Error bars represent standard errors of mean root biomass, n = 6



positively correlated with clay, and negatively with sand content, Ks, and depth to the B-horizon.

Rooting depth exhibited opposite results in that it was negatively correlated with clay, and positively with sand content, Ks, and depth to the B-horizon (Table 4; Fig. 6). The tallest trees were observed at sites with 0.8 m depth of the A horizon; tree height decreased with an increase in depth to the B-horizon. Regression analysis of depth to the B-horizon and tree height, canopy area, and total root biomass indicated that these relationships were well described by negative quadratic functions. Maximum rooting depth, on the other hand, increased with an increase in depth to the B-horizon, and

that was well described by positive quadratic functions (Fig. 6).

Discussion

Our study highlighted fundamental differences in root biomass distribution and whole-plant performance of a 10-year-old *H. ammodendron* plantation in duplex soils in a desert-oasis landscape. Properties of duplex soils, such as differing textures of A and B horizons, and depth of the A horizon, affect soil water infiltration and plant root growth (Tennant et al. 1992; Macinnis-Ng et al.

Table 4 Pearson correlations (r values) for tree growth characteristics versus soil properties (0-2 m) measured in 12 plots

	Root total biomass (kg m ⁻²)	Fine root biomass (kg m ⁻²)	Coarse root biomass (kg m ⁻²)	Tree height (cm)	Canopy area (cm ²)	Rooting depth (cm)
Sand component (%) Clay component (%) Bulk density (g cm ⁻³) Saturated hydraulic conductivity	$egin{array}{c} -0.87^{**} \\ 0.82^{**} \\ -0.78^{**} \\ -0.81^{**} \end{array}$	-0.51 0.56 -0.47 -0.48	$egin{array}{c} -0.88^{**} \\ 0.84^{**} \\ -0.78^{*} \\ -0.83^{**} \end{array}$	-0.80^{**} 0.83^{**} -0.79^{**} -0.86^{**}	$egin{array}{c} -0.81^{**} \\ 0.77^{*} \\ -0.71^{*} \\ -0.76^{*} \end{array}$	$\begin{array}{c} 0.97^{***} \\ -0.97^{***} \\ 0.97^{***} \\ 0.98^{***} \end{array}$
Ks (mm min ⁻¹) Saturated soil moisture content θ s (%) Capillary porosity (%) Depth of sandy surface layer (m)	0.75^{*} 0.77^{*} -0.83^{**}	$0.47 \\ 0.50 \\ -0.51$	0.81 ^{**} 0.79 ^{**} -0.85 ^{**}	0.82^{**} 0.77^{*} -0.84^{**}	0.77^{*} 0.66 -0.87^{**}	$\begin{array}{c} -0.98^{***} \\ -0.98^{***} \\ 0.97^{***} \end{array}$

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

2010). Changes in soil moisture after rainfall infiltration lead to physiological responses of *H. ammodendrom* (Eltahir 1998). Previous studies have indicated that light precipitation events might selectively favor shallowrooted plant species, and heavy rainfall events favor deep-rooted species in arid ecosystems (Dodd et al. 1998; Cheng et al. 2006). In duplex soils, soil water content of a deep silty-clay layer increased and remained high over an extended period after a large precipitation event (Fig. 4). Roots within or very close to the B horizon can access this stored water by direct uptake (Burgess et al. 2001, Macinnis-Ng et al. 2010).

Lower hydraulic conductivity in the subsoil (B-horizon) resulted from the higher content of clay, in agreement with other studies (Saxton and Rawls 2006; Jarvis et al. 2013). The silty-clay layer underlying the sand reduces the rate of deep percolation and increases the duration of water presence in the upper profile (Fig. 4), due to reduced hydraulic conductance and clay (Macinnis-Ng et al. 2010). Soil hydraulic conductivity controls water fluxes and storage, and, with that, a range of key eco-hydrological processes (Lebron et al. 2007; Lin, 2010). Plants growing in duplex soils developed special morphological adaptations of root systems which allowed the differentiation of plants response to rainfall between the duplex soils and uniform sandy soils. H. ammodendron growing in duplex soils may have an adaptive advantage to the changing water conditions of the future.

Roots of different diameters have different functional roles within the plant. Fine roots are predominately associated with water and nutrient uptake, while coarse roots may ensure additional functions of anchorage, transport, storage, and lateral root production (Plante et al. 2014). As expected, we found that the root biomass of *H. annodendron* significantly increased within or very close to the B horizon, especially for coarse root biomass, and fewer roots penetrated with depth. This behaviour likely reflected plant growth strategies in duplex soil. Root biomass concentrated in the upper sandy soil may allow plants to extract soil water during moist periods (Schenk and Jackson 2002; David et al. 2013). Plants growing in sandy soils can experience a higher water status than those grown in heavy-textured soils

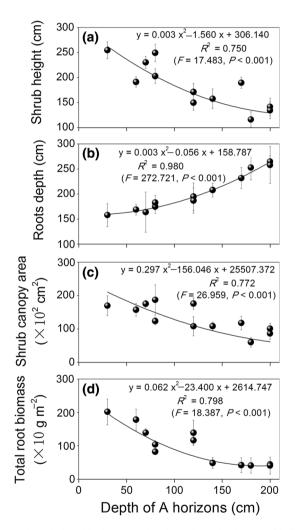


Fig. 6 The relationship between depth to the B-horizon and height (a), root depth (b), shrub canopy area (c), and total root biomass (d) of *Haloxylon annodendron. Error bars* represent standard errors of mean values

(Xu and Li 2008). However, the surface sandy-soil layer dries out during long periods without rain, potentially leaving plants without a water supply and rendering them vulnerable to xylem cavitation. Root biomass of *H. anmodendron* was very low in the top 20 cm of soil;

this layer is considered biologically-active. Due to the absence of water in the shallow soil layer, roots tended to extend down into the 0.5–1.0 m layer to obtain water from the deep soil. The plant could obtain enough water at depth to sufficiently offset the lack of it in the upper soil layer. This agrees with the mechanism proposed by Donovan and Ehleringer (1994), and Xu et al. (2007).

In addition, a deep B horizon containing a significant amount of clay can become saturated during large rainfall events (Chittleborough 1992). The dense subsoil clays form a barrier to root growth, and may also reflect the accumulation of water resources at the boundary between the A- and B-horizon (Laclau et al. 2001; Sudmeyer et al. 2004). Schenk and Jackson (2002) demonstrated that rooting depths largely depended on water availability, and predicted that rooting depth would increase when water was available at depth, and when transpirational demand increased. Thus, in uniform sandy soil profiles, plants would need extensive and deep root systems with a large surface area to facilitate water uptake from a large soil volume (Jackson et al. 2000, Xu and Li 2006). However, in duplex soils with sandy surface and clayey subsoil, plant root systems may respond to the texture of the B horizon with changes in root biomass distribution (Schenk and Jackson 2002). This strategy may reflect the accumulation of water and availability of other resources at the boundary between the sand and silty-clay layer (Sudmeyer et al. 2004).

Variable depth of the A-horizon in an H. ammoden*dron* plantation forest growing in duplex soils affects soil hydrology and consequently influences plant performance and community structure (Tennant et al. 1992; Hamerlynck et al. 2002). The species planted on active sand dunes 10 years ago exhibited significant differences in shoot size and rooting depth among plots (Fig. 6). The rooting penetration depth was positively correlated with depth of the A-horizon. On the contrary, total root biomass and shoot size were negatively correlated with depth of the A-horizon. Plants in plot 1 with the 30 cm depth of the A-horizon had the largest root biomass and shoot size. Maximum infiltration depths of most rainfall events were at the 0.2-0.5 m depths of the soil profile (Yang et al. 2014). Therefore, this combination of A and B horizons will benefit plant survival and growth. Sandy-surfaced horizon with high infiltration rates and low evaporation losses also increased water storage.

Duplex soils play an important role in promoting tree growth and maintaining the health of the planted forest. Two potential mechanisms promoted plant growth: (1) one, resulting from the large water storage capacity of the silty-clay layer, where plants can acquire enough water directly from the B horizon when depth to B horizon is less than 100 cm. This would be vital for facilitating the growth of plant shoots (Schenk and Jackson 2002). (2) If plants can acquire sufficient water, they can allocate photosynthetic products to the shoots and pursue maximizing aboveground production rather than expending energy for large root system construction and maintenance (Adiku et al. 2000; Xu et al. 2007). Trees may also be able to adjust their shoot and root system sizes toward an optimal phenotype that can maximize photosynthetic productivity and water availability (Schwinning and Ehleringer 2001; Xu et al. 2007) in duplex soils.

Conclusions

Texture and structure of the A and B horizons, and depth and variability in depth of the A horizon are important physical properties of duplex soils which influence the soil environment for root growth and water infiltration (Tennant et al. 1992). Root distribution of 10-year-old H. ammodendron plantation forest exhibited substantial variation among study sites with duplex soils. Young plants growing in duplex soils with a shallow A-horizon have an advantage in plant performance in limited water conditions. Knowledge of rootsystem development and whole-plant performance of young trees under various water regimes induced by soil texture will contribute to the development of suitable management scenarios and maintenance of forests planted to provide sand-stabilization in a desert ecosystem.

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