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Changes in soil and vegetation with stabilization of dunes in a desert–oasis ecotone

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Abstract Revegetation of indigenous plants in a desert–oasis ecotone is an effective way of maintaining the stability of oases. Understanding the changes in vegetation and soil is crucial for restoration management. The properties of soil and vegetation at stabilized sites of different ages were investigated in a typical desert–oasis ecotone, located in the Hexi Corridor region in arid northwestern China, over a period of 40 years. The results indicated that after 40 years the organic matter, total-N and available-P at 0–2 cm soil depth increased from 0.1, 0.1 g kg⁻¹, 7 mg kg⁻¹ to 2.0, 0.9 g kg⁻¹, and 75 mg kg⁻¹, respectively. At 2–5 cm the organic matter, total-N and available-P increased from 0.4, 0.1 g kg⁻¹, and 7 mg kg⁻¹ to 2.3, 0.4 g kg⁻¹, and 38 mg kg⁻¹, respectively. The number of herbaceous species increased from 4 to 9 and the herbaceous cover increased from 6 to 28 % after 40 years. The height and cover of the sand-binding vegetation *Haloxylon ammodendron* (*H. ammodendron*) reached the highest levels of 446 cm and 68 % after 25 years. After 35 years *H. ammodendron* dwindled and its belowground and aboveground biomass both decreased significantly. With effective natural regeneration, after 40 years the population of *H. ammodendron* remained stable and its cover and density remained at 38 % and 1870 ha⁻¹ respectively. The positive mutual feedback between vegetation and soil permitted the sand-binding vegetation community to become stable over time.

Keywords Desert–oasis ecotone · *Haloxylon ammodendron* · Herbaceous species · Plantation chronosequence · Soil properties

Introduction

The Hexi Corridor region is one of the main oasis regions in northwestern China, and its defining geomorphologic feature is that many oases of different shapes and sizes are interspersed in a wide sandy desert (Cheng et al. 1999). These man-made oases, which only represent a small portion of the land surface, are the centers for agricultural and human activity and play an important role in the economic and social development in this region. Because of the increasing human population and the overexploitation of soil resources by humans, desertification around oases has become the major obstacle for sustainable development of the oases, resulting in coarse, poor soil and low land productivity, exacerbating the problems of poverty and poor environmental quality.

A desert–oasis ecotone plays a prominent ecological role as an interactive zone between irrigated farmland and the natural desert ecosystem. Over the past several decades, ecological restoration in the ecotone zone has become the principle strategy for ensuring the ecological security of the overall oasis ecosystem in the Hexi Corridor region (Wang and Li 2013). Successful experiences pertaining to establishment of sand-protecting vegetation systems have been obtained in some areas of the desert–oasis ecotone (Su 2003; Wang et al. 2007). The recovery of sand-binding vegetation can effectively reduce the movement of mobile dunes and provide a favorable physical environment for the oasis (Su 2003). The practice of intensive re-vegetation over large areas has caused dramatic changes in soil, water and nitrogen, which might affect plant growth, distribution and vegetation structure (Chapin et al. 1986; Berndtsson and Chen 1994; Berndtsson et al. 1996; Wedin and Tilman 1996; Aguiar and Sala 1999; Dale and Adams 2003; Oztas et al. 2003; Schwinning et al. 2004). Maintaining a stable desert–oasis ecotone has become a key issue for sustainable development of the oasis ecosystem in the Hexi Corridor region. Monitoring the dynamics of sand-

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binding vegetation and soil has been inadequate to date. More information is needed for a better understanding of the restoration mechanisms and the interactions between soil and plant communities, and for appropriate management and conservation measures (Wortley et al. 2013). This study presents a typical case of successful ecological restoration efforts in the Hexi Corridor, which is representative of an oasis–desert ecotone area in arid regions with an annual precipitation of around 120 mm.

The aim of this study was to investigate the dynamics of a sand-binding shrub *Haloxyton ammodendron* (*H. ammodendron*) plantation over a 40-year period and to improve our knowledge of the restoration of desert communities in arid desert lands. The specific objectives were: (a) to record the changes in soil water content, soil fertility properties, vegetation species composition, cover, and biomass over a 40-year period; (b) to assess the stabilization mechanism of sand-binding vegetation communities for sand dunes.

Materials and methods

Study sites

The study sites, covering the Pingchuan marginal oasis (39°21'N and 100°21'E, at 1367 m above mean sea level a.m.s.l.), in Linze county in the middle of the Hexi Corridor area, are located in a typical desert–oasis ecotone at the southern fringe of the Badain Jaran Desert. The climate in this area is a typical temperate desert climate: dry and hot in summer, cold in winter, strong winds and frequently drifting sand. The mean annual air temperature is 7.6 °C, with an absolute maximum of 39.1 °C in summer and an absolute minimum of –27 °C in winter. The annual mean precipitation is 117 mm, while the annual mean potential evaporation is 2390 mm. The mean annual wind velocity is 3.2 ms^{–1} and the prevailing wind direction is northwest. Gales with wind velocity above 17 ms^{–1} occur mainly in spring for about 15 or more days per year. The main soil types are Aripsamment and Calciorthiss with loose structure and low organic matter, and are very susceptible to wind erosion (Chen et al. 1998).

Ecological restoration

Sandy desertification caused by wind and sand activities has become the main form of land desertification in the study area. Vegetation degradation in arid regions is one of the major causes of desertification and the original fixed shrubby sand dunes were mobilized because of overexploitation and irrational reclamation of land in oases (Zhang et al. 2003). *Haloxyton ammodendron* is native to a variety of central Asian desert habitats where annual rainfall ranges from 30 to 200 mm. It can adapt to harsh environments by minimizing water loss and

maximizing productivity to stay alive and even to thrive in desert areas (Chesson et al. 2004; Schwinning et al. 2004; Xu and Li 2006). Because of its remarkable tolerance to drought and ability to survive in arid areas, *H. ammodendron* has been widely used as a pioneer species to prevent desertification in the Hexi Corridor region (Zou et al. 2010). In the study area, seedlings of *H. ammodendron* were planted without irrigation as the main anti-sandstorm shrub, to increase soil cover and reduce wind erosion. Revegetation areas were expanded one by one along the mobile dunes in 1973, 1978, 1988, 1998, 2006 and 2010 using the same method. *Haloxyton ammodendron* gradually became the dominant species and with the development of this sand-binding vegetation community, the mobile dunes have been effectively stabilized. The rate of shifting sand has declined from 54.6 % in the pre-plantation state to 9.4 %, and the success of this effort has also played an important role in the restoration of the local eco-environment (Research Group of “Study on Combating Desertification/Land Degradation in China” 1998).

Field investigation

Investigation of vegetation status

A substitution method of “space” for “time” is normally considered a reliable way to monitor and study changes over long time periods (Sparling et al. 2003). The investigation of the vegetation was performed in August 2013. Fourteen different sites were selected to quantitatively describe the change in soil and vegetation in an age series of 3-, 7-, 15-, 25-, 35- and 40-year stabilized sites (Fig. 1). Forty-two shrub quadrats of 25 × 25 m² and 210 herb quadrats of 1 × 1 m² were set up at the six different-aged sites (three shrub quadrats at each site and five herb quadrats at each shrub quadrat were randomly selected). All the selected sites were on flat land, and the separation distance between each of the shrub quadrats was greater than 50 m (Fig. 2). Morphological traits of *H. ammodendron* of different plantation ages were measured, including the diameters of base stems, the canopy widths and the heights (Table 1). The roots of the planted *H. ammodendron* were excavated to investigate their vertical distribution in sites of 3, 7, 15, 25, and 35 years stabilization. Three individuals of *H. ammodendron* with similar canopy sizes and approximately average heights were randomly selected for excavation, and their aboveground biomasses were measured, in each site. As a deep-rooted plant, the shape of the *H. ammodendron* root system resembles a cylinder, and the feeder roots of *H. ammodendron* primarily develop vertically and only rarely laterally (Sheng et al. 2004). Fine roots with diameters of less than 2 mm were generally defined as feeder roots for water and mineral uptake, but they are difficult to collect and record (Gordon and Jackson 2000), as they can be easily broken away when the soil is manually removed. In this

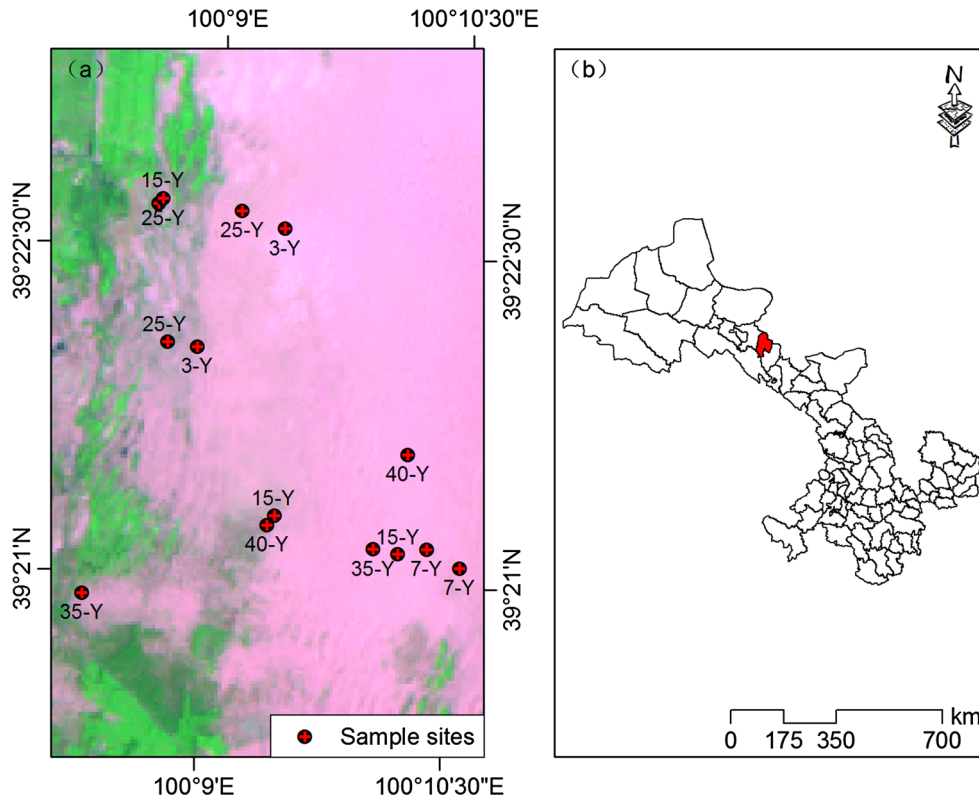


Fig. 1 Map of the study area **a** Fourteen different sites in the study area (3-Y represents 3-year, 7-Y represents 7-year, 15-Y represents 15-year, 25-Y represents 25-year, 35-Y represents 35-year, 40-Y represents 40-year, *green* represents vegetation and *purple* represents bare land). **b** Location of the study area in Gansu Province

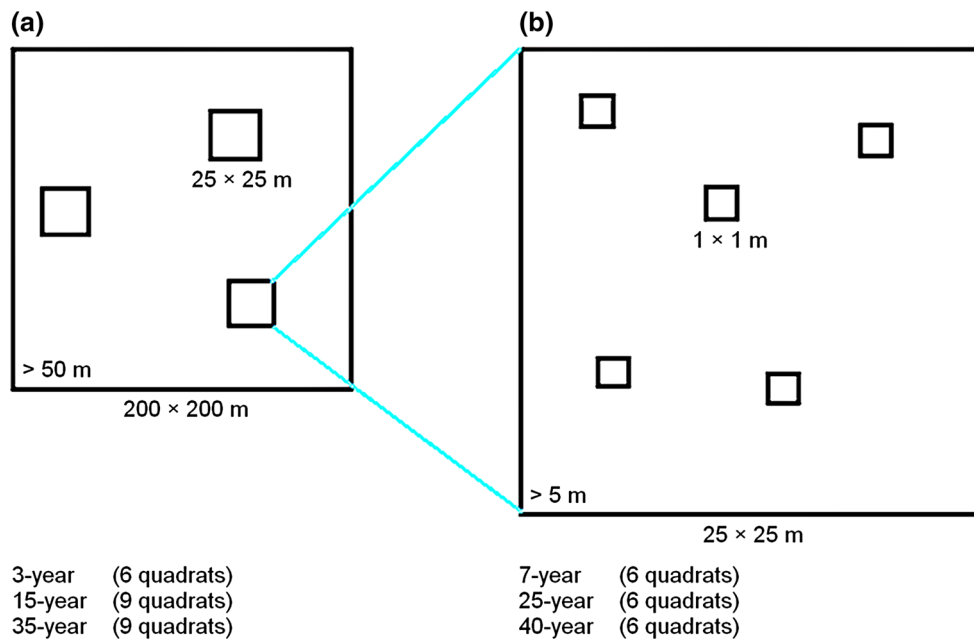


Fig. 2 Shrub and herbaceous quadrat design: **a** Three shrub quadrats in the area of $200 \times 200 \text{ m}^2$. **b** Five herbaceous quadrats in every shrub quadrat

study, soil cylinders with diameters of 100 cm surrounding the main root were collected manually at 20-cm intervals. The diameter of the root was measured with a caliper. Roots with decayed surfaces were not

recorded, as they had lost the ability to grow the fine roots required to absorb water. The aboveground biomass was separated into leaves, branches and stems. All samples were oven-dried at $80 \text{ }^\circ\text{C}$ until consistent

Table 1 Morphological traits of *Haloxylon ammodendron* by plantation age

Traits	Plantation age (years)					
	3	7	15	25	35	40
Diameter of base stem (cm)	6.3 ± 0.4a ^{a,b}	13.18 ± 2.3b	18.6 ± 0.8d	25.9 ± 1.1f	20.7 ± 0.8e	15.6 ± 0.8c
Canopy width (m ²)	0.9 ± 0.3a	1.5 ± 0.2a	3.6 ± 0.4b	4.6 ± 0.4c	3.8 ± 0.3b	3.5 ± 0.9b
Height (cm)	84.8 ± 8.0a	154.0 ± 14.8b	271.2 ± 19.8c	445.8 ± 56.8e	381.8 ± 33.5d	363.0 ± 29.6d

^a Values are means ($n = 30$) ± standard deviation

^b Differences in morphological traits of *H. ammodendron* in sites of different stabilization ages were examined using one-way ANOVA. Different letters represent significant differences across stabilization years from post hoc Duncan tests ($P < 0.05$)

weights were attained. Herbaceous density and cover were recorded for each species in each herb quadrat. Aboveground biomass of the herbaceous layer was clipped above ground in a 1 × 1 m quadrat, replicated 5 times, in each plot. The aboveground biomass of different herb species was collected and measured by dry weight.

Measurement of soil development

Soil water status was measured at the end of September when the main rainfall season was over. According to the soil water status and the distribution of plant root systems in the study area, the soil profile of 0–200 cm depth was divided into three layers from top to bottom: top active layer (10–50 cm), shallow sub-active layer (50–100 cm) and deep stable layer (100–200 cm). The soil at depths of 10, 50, 100 and 200 cm was sampled with three replicates at three random positions in each shrub quadrat, using an auger. To describe the soil water status in the sites of different ages, 504 soil samples were measured by a conventional weighing method. Five soil samples of 0–2 and 2–5 cm were randomly collected and mixed into a composite sample within the sampling plots at each site. Soil organic matter (SOM) was determined by the dichromate oxidation method of Walkley–Black (Nelson and Sommers 1982), total nitrogen (total-N) was measured by the micro-Kjeldahl procedure and available-P by the Bray method (Institute of Soil Sciences, and Chinese Academy of Sciences 1978).

Statistical analysis

Data analysis and charting were performed using the statistics software Origin 8.0 (OriginLab Corp., Northampton, MA, USA). Linear stepwise regression was used to determine the correlation between vegetative features and soil parameters. Analyses were performed using the Windows-based SPSS software (10th edn; SPSS, Chicago, IL, USA). Descriptive statistics were used to calculate means and standard deviations for each set of duplicates. One-way analysis of variance (ANOVA) was used to test for significance differences of soil water content in different sites from post hoc Duncan tests.

Results

Soil water and nutrient changes following stabilization of sand dunes

The soil water content at various depths (10, 50, 100 and 200 cm) changed with time since stabilization (Fig. 3). Except for the soil at 50 cm, there were no significant differences among the sites of different ages (Fig. 3). In the soil at 50 cm, the soil water content in the mobile dunes was significantly higher than in the revegetated areas (Fig. 3b). The mean soil water content decreased from an initial 3.3 % in the mobile dunes to 1.5 % in the stabilized dunes after 40 years (Fig. 3b).

Soil organic matter (SOM), total-N and available-P all increased significantly with time after revegetation for the topsoil at 0–2 and 2–5 cm (Fig. 4a–c). SOM at 0–2 cm increased from 0.1 to 2.0 g kg⁻¹, and at 2–5 cm from 0.4 to 2.3 g kg⁻¹. Total-N at 0–2 cm increased from 0.1 to 0.9 g kg⁻¹, and at 2–5 cm from 0.1 to 0.4 g kg⁻¹. Available-P at 0–2 cm increased from 7 to 75 mg kg⁻¹, and at 2–5 cm from 7 to 38 mg kg⁻¹. The rate of increase in soil nutrients was greater at 0–2 cm than at 2–5 cm (Fig. 4a–c). The relative percentage of soil cations K, Na, Ca and Mg at 0–2 cm changed from 6, 18, 66 and 10 to 10, 78, 6 and 6 %, respectively. The relative percentage of soil cations K, Na, Ca and Mg at 2–5 cm changed from 4, 26, 55 and 15 % to 14, 70, 9 and 7 %, respectively. The dominant cation at 0–2 and 2–5 cm changed from Ca²⁺ to Na⁺ (Fig. 5a, b).

Vegetation dynamics following stabilization of sand dunes

Changes in *H. ammodendron* morphological traits and density

The diameters of base stem, canopy widths and heights of plants of different *H. ammodendron* plantation ages varied significantly (Table 1), increasing with time from 3 years to 25 years and reaching their highest levels of 25.9 cm, 4.6 m² and 445.8 cm, respectively, after 25 years. After 35 years they began to decrease and after 40 years they had decreased to 15.6 cm, 3.5 m² and 363.0 cm, respectively (Table 1).

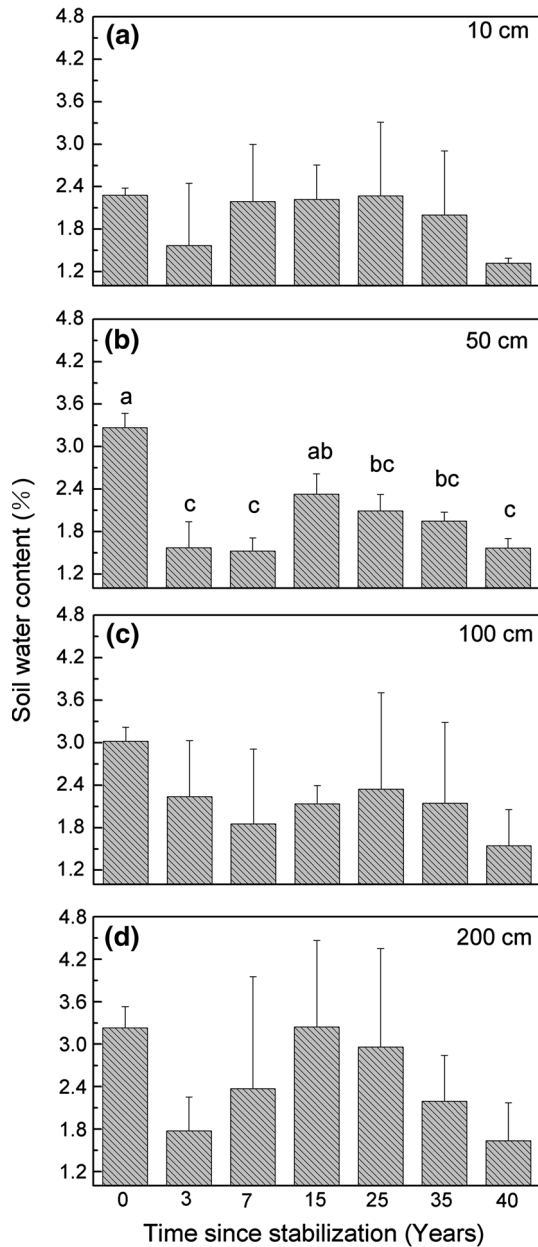


Fig. 3 Mean soil water content at depths of **a** 10 cm, **b** 50 cm, **c** 100 cm and **d** 200 cm as affected by time since stabilization of sand dunes. *Error bars* represent the standard deviations of the means. Differences in mean soil water content in sites of different stabilization ages were examined using one-way ANOVA; *different letters* represent significant differences among stabilization years from post hoc Duncan tests ($P < 0.01$)

After revegetation, the density of planted *H. ammodendron* decreased dramatically, from 2859 ha⁻¹ after 3 years to 187 ha⁻¹ after 40 years (Fig. 6a). *Haloxylon ammodendron* cover increased with time from 3 years to 25 years, reaching the highest level of 68 % after 25 years, and then decreasing steadily. After 40 years, the cover remained at 28 % (Fig. 6b). The underground and aboveground biomass of *H. ammodendron* changed consistently, increasing with time from 3 to 25 years,

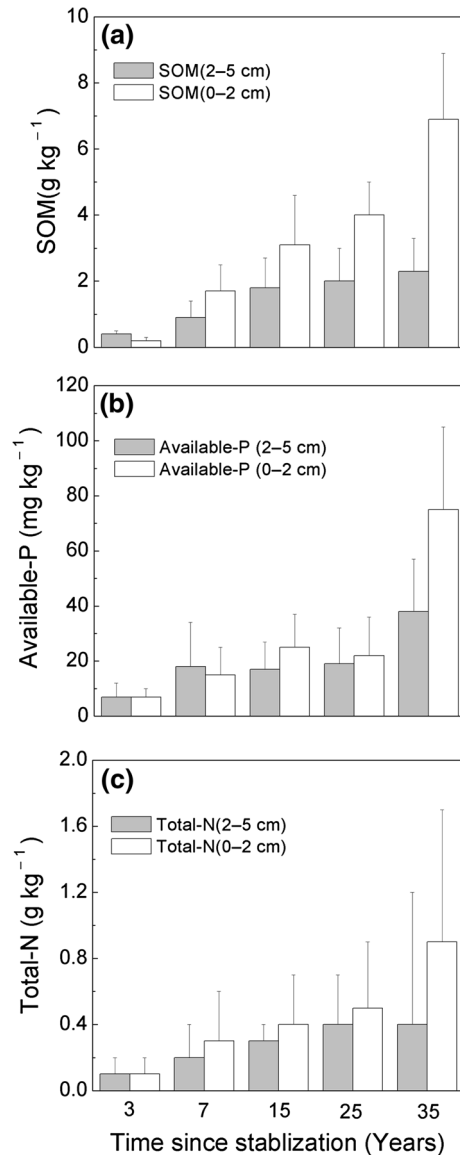


Fig. 4 Changes in soil nutrients in topsoil at 0–2 and 2–5 cm compared with time since stabilization of sand dunes: **a** soil organic matter (SOM), **b** total-N and **c** available-P. *Error bars* represent the standard deviations of the means

reaching their highest levels after 25 years, and then decreasing after 35 years (Figs. 7, 8).

Except for *H. ammodendron*, no other shrub species was found to have germinated and established naturally in the sand-binding vegetation community after the 40-year succession period. The increasing trend of the density and cover of the regeneration sites was significant (Fig. 6c, d). After 40 years, the density and cover reached 1750 ha⁻¹ and 9 %, respectively (Fig. 6c, d).

Changes in herbaceous species

With the stabilization of the sand dunes, the number, species richness, biomass and cover of herbaceous plants

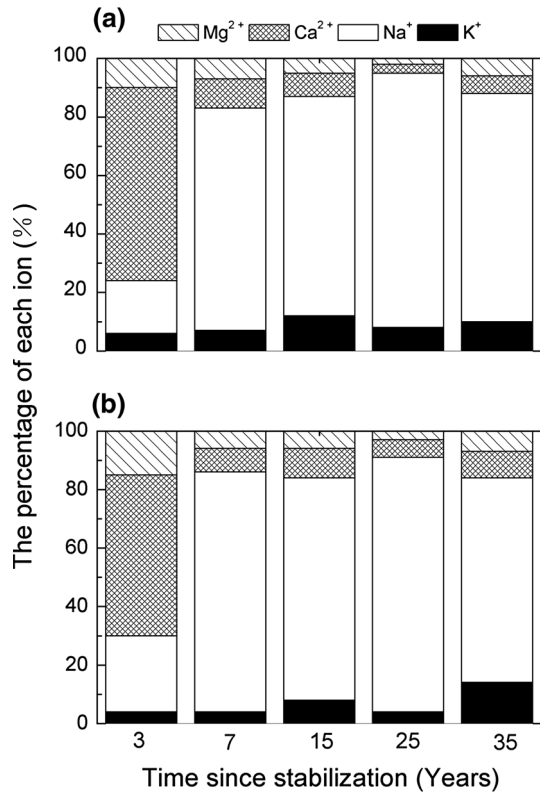


Fig. 5 Changes in soil cations in topsoil at 0–2 and 2–5 cm compared with time since stabilization of sand dunes: **a** soil cations in 0–2 cm and **b** soil cations in 2–5 cm

all increased linearly with time (Table 2). The density of herbaceous plants increased from 12 m⁻² after 3 years to 249 m⁻² after 40 years; the number of species increased from 4 to 9; the biomass increased from 2.8 g m⁻² after 3 years to 56.4 g m⁻² after 40 years; and the cover increased from 6 to 28 % over a period of 40 years (Table 2).

Discussion

Desert soils in an arid rain-fed environment have low silt and clay content, and are therefore low in available water to support plant growth (Saxton and Rawls 2006). In arid ecosystems, soil moisture is the most important abiotic factors influencing the growth of plants and the composition of plant communities (Smith et al. 1997). Changes in soil moisture in re-vegetated areas have been recognized as one of the major processes influencing the establishment and persistence of sand-binding vegetation in arid lands (Rietkerk et al. 2004; Ursino 2009). Planting deep-rooted shrubs for sand dune stabilization can cause deterioration of soil moisture at the greater depths of 100–300 cm because of the large water consumption of the sand-binding vegetation (Li et al. 2004). In this study, the decrease in soil moisture occurred at the shallow depth of 50 cm rather than at the deeper depths of 50 cm rather than at the deeper depths of 50 cm (Fig. 3), because the feeder roots of *H. ammodendron* were distributed mainly in the shallow layers

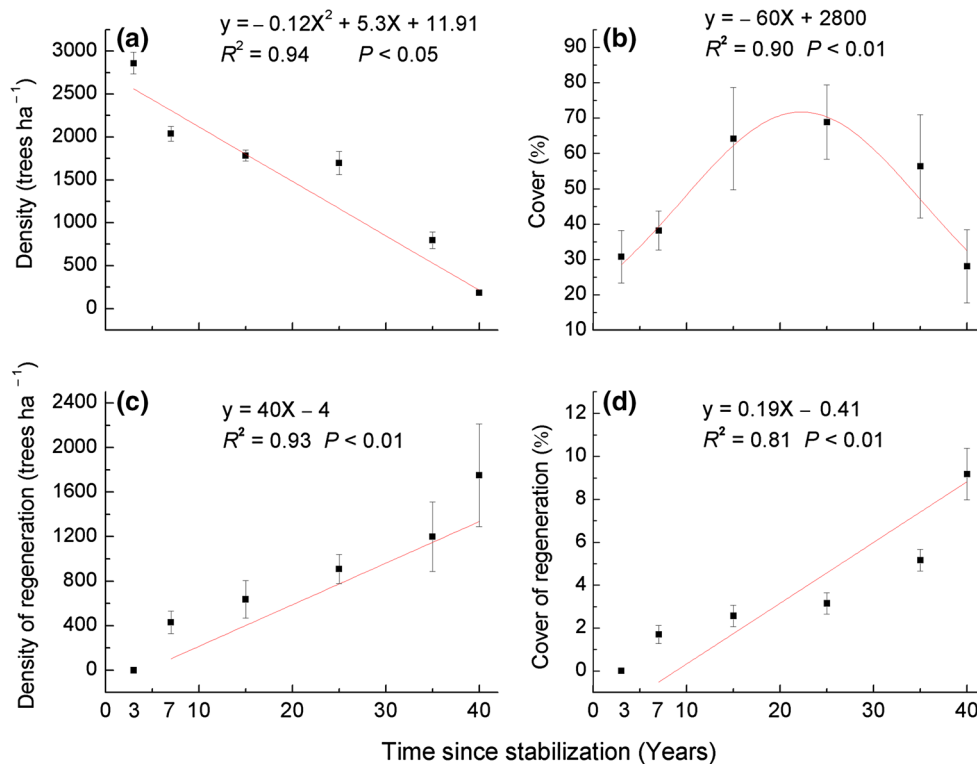


Fig. 6 Changes in *H. ammodendron* density and cover over time since stabilization of sand dunes **a** density, **b** cover of planted *H. ammodendron*, **c** density and **d** cover of regenerated *H. ammodendron*. Error bars represent the standard deviations of the means

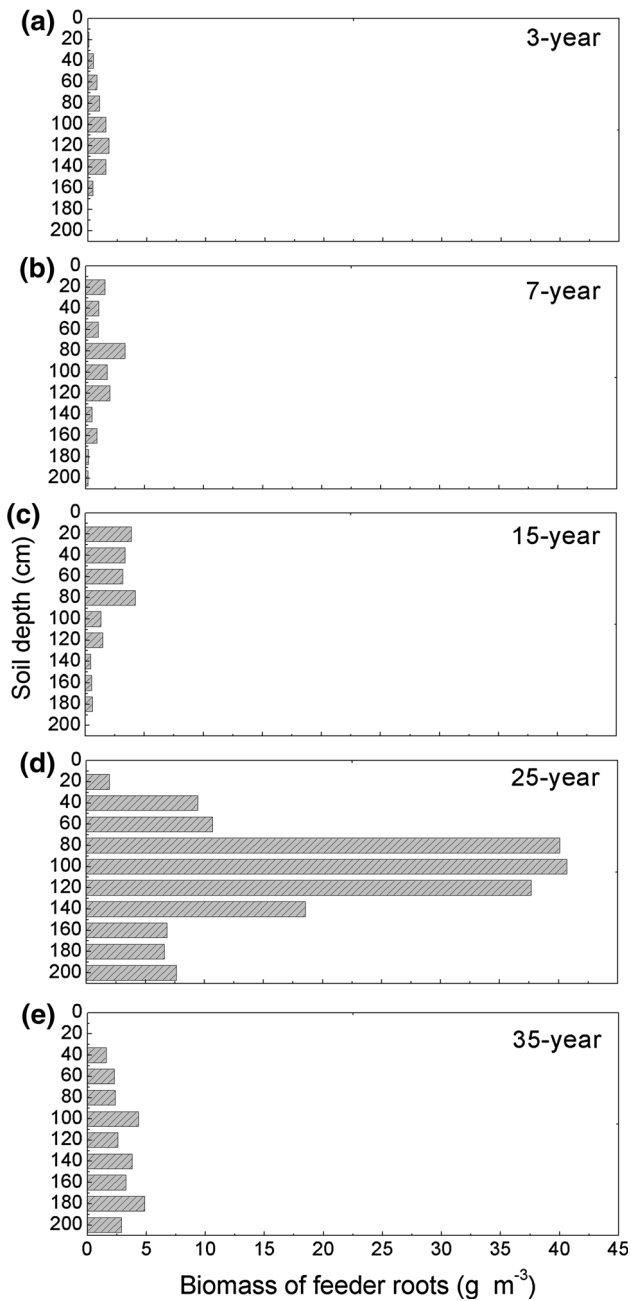


Fig. 7 Distribution of feeder roots of *H. ammodendron* in sites of different ages **a** 3-year, **b** 7-year, **c** 15-year, **d** 25-year and **e** 35-year

from 50–90 cm. This result agrees well with Xu and Li (2006). Soil moisture at 50 cm was also the main physical factor influencing the cover of *H. ammodendron* (Table 3). These results confirm that *H. ammodendron* can use shallow soil water as its main water resource. Soil water at shallow depths can be replenished from rainfall, providing a reliable water resource for the growth of *H. ammodendron* in arid areas (Breshears and Barnes 1999; Loik et al. 2004).

Because of long-term wind erosion on mobile sand dunes, the soils have very high sand content with low soil water and nutrient status (Buckley et al. 1986).

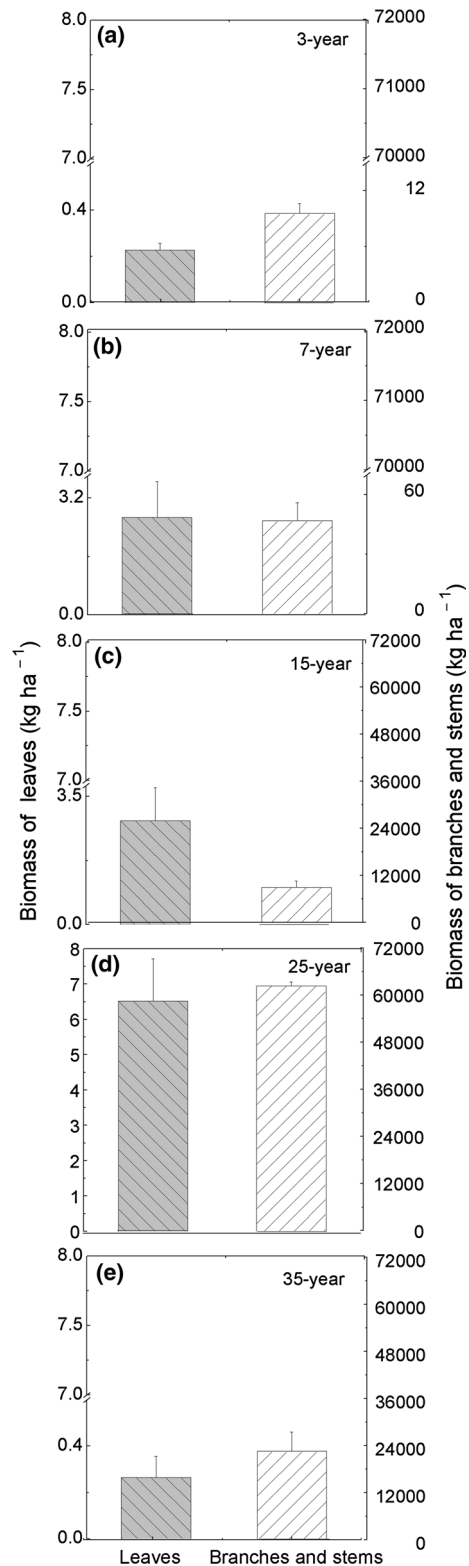


Fig. 8 Aboveground biomass of *H. ammodendron* in sites of different ages **a** 3-year, **b** 7-year, **c** 15-year, **d** 25-year and **e** 35-year. Error bars represent the standard deviations of the means

Planting indigenous shrubs to build a vegetation sand-binding system can function as a natural barrier to reduce wind velocity and prevent the erosion of near-

Table 2 Species composition of artificial *H. ammodendron* communities of different ages

Species name	Life form	Time period of stabilization (years)								
		3	7	15						
		D (m ⁻²)	F (%)	B (g m ⁻²)	D (m ⁻²)	F (%)	B (g m ⁻²)	D (m ⁻²)	F (%)	B (g m ⁻²)
<i>Bassia dasyphylla</i>	AF	2 ± 1	93	1.8 ± 0.6	33 ± 15	97	2.7 ± 1.0	99 ± 52	100	7.4 ± 3.0
<i>Agriophyllum squarrosum</i>	AF	7 ± 3	68	0.7 ± 0.3	14 ± 5	62	0.3 ± 0.1	1 ± 0	3	0.1 ± 0
<i>Halogeton arachnoideus</i>	AF	2 ± 1	20	0.2 ± 0.1	3 ± 1	11	3.2 ± 3.0	19 ± 12	66	2.4 ± 1.0
<i>Eragrostis pilosa</i>	AG	1 ± 0	3	0.1 ± 0	5 ± 0	2	5.5 ± 0	5 ± 2	20	0.1 ± 0.1
<i>Salsola collina</i>	AF				2 ± 1	15	0.2 ± 0.1	2 ± 1	37	0.7 ± 0.3
<i>Chloris virgata</i>	AG							3 ± 0	3	0.1 ± 0
<i>Salsola ruthenica</i>	AF				5 ± 4	4	0.4 ± 0.2	1 ± 0	3	0.2 ± 0
<i>Corispermum macrocarpum</i>	AF									
<i>Setaria viridis</i>	AG									
<i>Artemisia scoparia</i>	AF									
<i>Zygophyllum fabago</i>	PG									
Density (m ⁻²)		12			62			130		
Biomass (g m ⁻²)		2.8			12.3			11.0		
Total species number		4			6			7		
Coverage (%)		5.8 ± 1.0			5.4 ± 0.8			16.2 ± 0.9		
Species name	Life form	Time period of stabilization (years)			Time period of stabilization (years)			Time period of stabilization (years)		
		25	35	40						
		D (m ⁻²)	F (%)	B (g m ⁻²)	D (m ⁻²)	F (%)	B (g m ⁻²)	D (m ⁻²)	F (%)	B (g m ⁻²)
<i>Bassia dasyphylla</i>	AF	88 ± 29	91	3.7 ± 2.0	46 ± 20	100	6.7 ± 3.0	87 ± 38	37	18 ± 11
<i>Agriophyllum squarrosum</i>	AF	5 ± 1	7	1.6 ± 0.8	124 ± 86	7	10.2 ± 2.0	6 ± 3	23	0.5 ± 0.3
<i>Halogeton arachnoideus</i>	AF	22 ± 10	76	1.7 ± 1.0	21 ± 10	64	3.5 ± 3.0	10 ± 3	33	6.8 ± 2.0
<i>Eragrostis pilosa</i>	AG	28 ± 5	6	1.3 ± 0.6	32 ± 10	20	2.9 ± 1.0	13 ± 5	17	3.6 ± 1.0
<i>Salsola collina</i>	AF	3 ± 2	11	2.4 ± 1.3	4 ± 2	23	3.3 ± 2.3	5 ± 2	6	1.6 ± 0.5
<i>Chloris virgata</i>	AG	3 ± 1	9	5.1 ± 1.3	123 ± 70	3	9.5 ± 2.3	120 ± 50	3	5.0 ± 3.4
<i>Salsola ruthenica</i>	AF				2 ± 1	10	0.9 ± 0.7	3 ± 0	3	0.4 ± 0
<i>Corispermum macrocarpum</i>	AF	5 ± 4	7	0.4 ± 0.3	16 ± 10	10	5.1 ± 3.4	2 ± 1	10	0.5 ± 0.3
<i>Setaria viridis</i>	AG				2 ± 1	10	0.3 ± 0.1	3 ± 2	20	20 ± 10
<i>Artemisia scoparia</i>	AF									
<i>Zygophyllum fabago</i>	PG	7 ± 0	2	0.6 ± 0	22 ± 20	27	3.6 ± 1.9			
Density (m ⁻²)		161			392			249		
Biomass (g m ⁻²)		16.8			46			56.4		
Total species number		8			10			9		
Coverage (%)		13.9 ± 1.9			17.5 ± 1.6			27.5 ± 1.5		

D density (m⁻²), F frequency (%), B biomass of herbaceous plants (g m⁻²), AF annual forb, AG annual grass, PG perennial grass

Table 3 Stepwise regression analysis for soil parameters and vegetative features over time and after sand stabilization

Equations	F	P
<i>Haloxylon ammodendron</i> cover = 46.98 soil water content (50 cm) – 35.14	14.40	<0.05
Regenerated <i>H. ammodendron</i> density = 124.51 SOM (0–2 cm) + 55.26	21.59	<0.05
Herbaceous density = 53.76 SOM (0–2 cm) – 16.73	42.69	<0.01
Herbaceous species richness = 0.29 SOM (0–2 cm) + 2.21	29.54	<0.05
Herbaceous biomass = 6.11 SOM (0–2 cm) – 1.78	23.30	<0.05

SOM represents soil organic matter

surface soil. This provides a stable soil-forming environment, and once the mobile dunes have stabilized, the enrichment of dune surfaces through aeolian deposition of fine particles becomes an important process of pedogenesis. Large amounts of silt-sized particles (0.01–0.05 mm) were deposited on the sand surface and as reported the amount of fine particles falling from the atmosphere every year is about 0.8–2.0 mm in the desert area of northern China after sand-binding vegetation establishment (Lin and Qu 1993; Zhao et al. 2007). The wind-deposited particles have increased the proportion of fine-sized silt and clay in topsoil year by year and have thereby altered the original soil mechanical composition (Wezel et al. 2000; Hupy 2004; Cao et al. 2008; Dong et al. 2009). Shifting sand is no longer the only soil substrate, and transported fine materials play a more important role in altering soil texture. In the Horqin Sand Land with the establishment of sand-binding vegetation the contents of clay and silt increased by 13.9 times and the SOM and total-N in the topsoil increased to 35 and 1.0 g kg⁻¹ after 15 years (Zhao et al. 2011). In the Tengger Desert the contents of clay and silt increased by 8.8 times after 30 years and the SOM and total-N in the topsoil increased to 8 and 0.7 g kg⁻¹ after 40 years (Li et al. 2002, 2007). In our study area, with establishment of *H. ammodendron*, the contents of silt and clay in the surface layer increased 3 times and 2 times, respectively, and the fine-particle fractions of silt and clay reached 9 % (Su et al. 2010). After 40 years the organic matter and total-N at the surface increased from 0.1 and 0.1 to 2.0 and 0.9 g kg⁻¹, respectively (Fig. 4).

The soil nutrient enrichment process in our study area was slow in comparison with other deserts of northwest China. We interpret this difference as resulting primarily from the lower rate of silt and clay accumulated on the sand dunes in our study area (Drees 1993). We also found that the dominant soil cation at 0–2 and 2–5 cm changed from Ca²⁺ to Na⁺ (Fig. 5a, b). *Haloxylon ammodendron* can absorb and accumulate Na⁺ from sand, largely in its leaves and branches, as an effective osmotic agent to adapt to arid environments (Wang et al. 2004; Kang et al. 2013). With the self-thinning process and dwindling of *H. ammodendron*, large amounts of leaf and branch litter became the main Na⁺ source for the surface soil.

With the establishment of sand-binding vegetation, the surface soil fertility was significantly improved, creating a favorable environment for the germination and

establishment of shallow-rooted annual forbs and grasses (Table 3). After 3 years of re-vegetation, *Bassia dasyphylla*, *Agriophyllum squarrosum* and *Halogeton arachnoideus* began to invade and establish themselves in the stabilized dunes. From 7 to 25 years more and more other annual herbs and grasses gradually invaded and became established, and the biomass, density, species numbers and coverage of herbaceous species all increased with time. After 40 years, the number of herbaceous species settled in the study area reached 9, the density increased to 249 m⁻² and the cover increased to 28 % (Table 2). *Bassia dasyphylla* was the first invading species and after 40 years it became the dominant annual herbaceous species (Table 2). Its density and biomass reached 87 m⁻² and 18 g m⁻², respectively. *Zygophyllum fabago* was the only perennial grass that invaded stabilized dunes after 25 years (Table 2). The species of invading herbaceous plants were mainly annual forbs and grasses.

As a reservoir for essential elements, SOM is a key indicator of soil nutrients and its accumulation can indicate an improvement in soil fertility (Brooks 2003). Although the rate of increase of SOM in our study was slow, it played an important role in plant colonization and establishment—especially the improvement of SOM at 0–2 cm—thereby promoting the development of herbaceous species and increasing the density, biomass and number of species over time (Tables 2, 3). The rapid growth and death of herbaceous plants subsequently promoted the cycle of soil fertility (Christensen 2001). In this study, SOM, total-N and available-P in the topsoil were most strongly affected by herbaceous biomass, which accounted for 89, 95 and 94 % of their variation, respectively (Fig. 9a–c). Herbaceous density was the other important factor affecting SOM and total-N in the topsoil (Fig. 9d, e). Our results suggested that increased herbaceous plant density affected soil nutrients mainly through increased productivity. This feedback between herbaceous plants and soil formed a mutually beneficial mechanism for the development of surface soil and annual species.

Over the period of 3–25 years, *H. ammodendron* grew very quickly and after 25 years the height and cover reached their highest levels of 446 cm and 68 % (Table 1; Fig. 6b). After 25 years the *H. ammodendron* population began to dwindle and after 35 years it degenerated to the point of death. The decline was especially noticeable in the root system with the feeder root

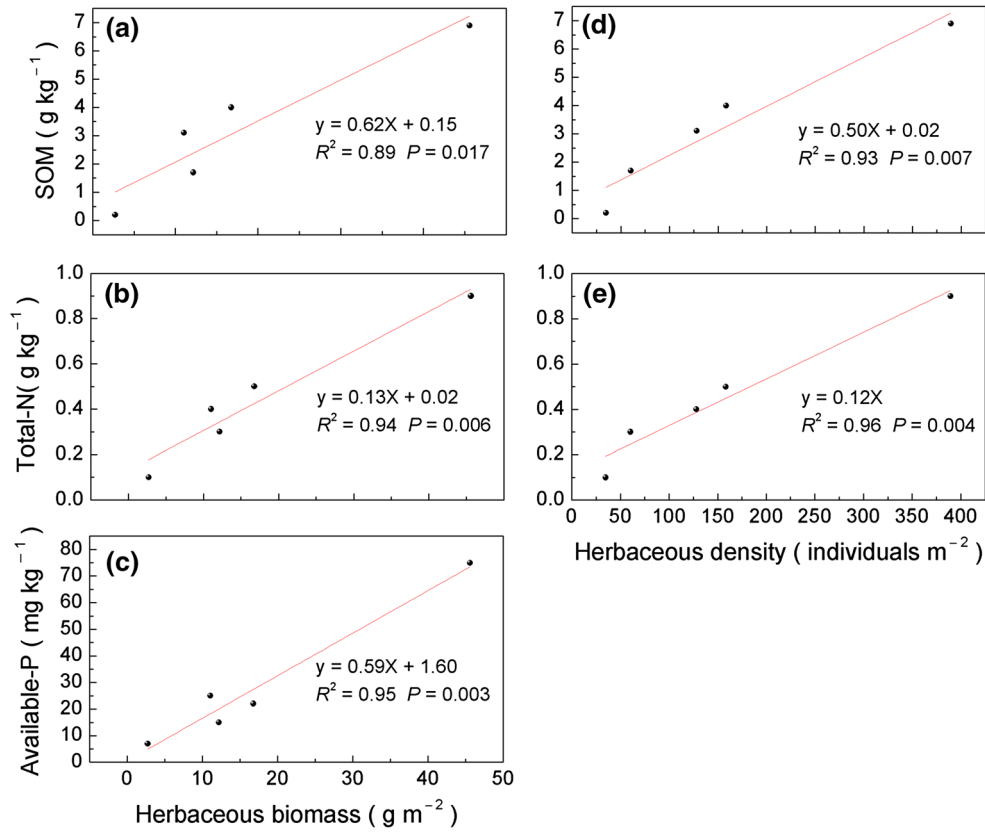


Fig. 9 Relationships between herbaceous biomass and **a** soil organic matter (SOM), **b** Total-N, **c** Available-P, and relationships between herbaceous density, **d** SOM and **e** Total-N

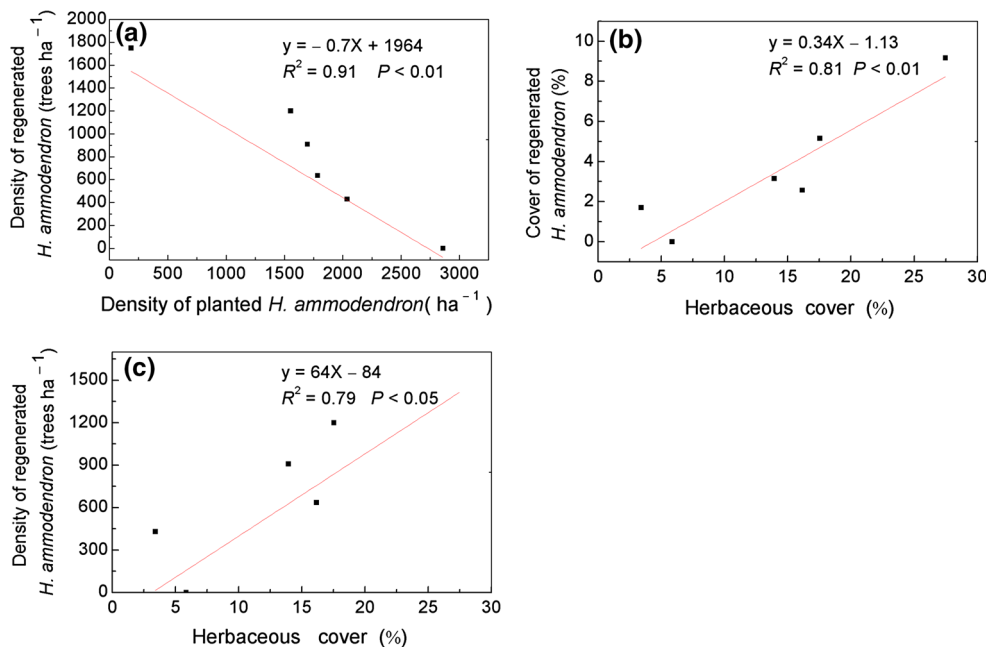


Fig. 10 Relationships between **a** density of regenerated *H. ammodendron* and planted *H. ammodendron*; **b** cover of regenerated *H. ammodendron* and herbaceous cover; and **c** density of regenerated *H. ammodendron* and herbaceous cover

biomass in the plants measuring from 0 to 200 cm decreasing significantly after 35 years (Fig. 7e). Typically, the root system of desert shrubs is closely related to water availability. With the increasing revegetation over time, the available soil water in shallow depths significantly decreased. Water deficit can lead to the deterioration of feeder roots in shallow depths (Sperry and Hacke 2002). Besides the lack of available water, the weakening of physiological drought-resistance is the other reason for the degeneration of *H. ammodendron*. Some studies have demonstrated that the root system of *H. ammodendron* needs a large amount of Na^+ and K^+ , which could work as osmotic regulation substances, to maintain lower root water potential and significantly mitigate the deleterious impacts of drought stress on growth (Kang et al. 2013). Over time, the Na^+ and K^+ in the soil were absorbed by *H. ammodendron* and then concentrated at the surface forming a salt crust. The scarcity of Na^+ and K^+ in the soil directly leads to a reduction in the ability to avoid drought stress. Under conditions of water deficit and without significant drought-resistance, the below-ground biomass decreased significantly after 35 years. The biomass of leaves began to decrease concurrently with the decrease in biomass of feeder roots to reduce the water loss from transpiration (Fig. 8e). Consequently the photosynthesis and productivity of *H. ammodendron* were weakened, leading to a dramatic decrease in the biomass of stems and branches (Tables 1; Fig. 8e).

After 40 years the density and cover of planted *H. ammodendron* decreased to 187 ha^{-1} and 28 % (Fig. 6a, b), but the regeneration of *H. ammodendron* maintained the population and stabilized its function as sand-binding vegetation. Because of shading effects, many plants seem unable to establish new individuals directly underneath adults of the same species, and indeed the density of planted *H. ammodendron* was negatively related to the density of regenerated *H. ammodendron* (Fig. 10a). *Haloxylon ammodendron*, as a C_4 plant, needs adequate sunshine and space to survive (Su et al. 2007). With the self-thinning and degeneration characteristics of planted *H. ammodendron*, the stress of space for regeneration was gradually eliminated. After 40 years the density and cover of regenerated *H. ammodendron* reached 1750 ha^{-1} and 9 % (Fig. 6). The increase in SOM at 0–2 cm was beneficial for the development of regeneration (Table 3). Because herbaceous plants can accelerate the cycle of soil nutrients and provide a mild and humid near-surface environment for *H. ammodendron* seeds, the development of herbaceous species was also beneficial for the regeneration of *H. ammodendron* (Fig. 10b, c). After 40 years, the density and cover of *H. ammodendron* remained at 1870 ha^{-1} and 38 %.

In conclusion, after 40 years, the shrub layer of *H. ammodendron* was stabilized through effective regeneration. The herbaceous cover, diversity, density and biomass all increased with plantation age. The simple, sand-binding vegetation system developed towards a complex semi-natural ecosystem with a multi-layered

structure. There was a clear linear increasing trend for soil nutrient recovery in response to vegetation recovery primarily because of the improving herbaceous productivity. The magnitude of the increase declined with depth and the improvement mainly occurred at the surface soil level, with nutrient recovery at deeper depths requiring longer time periods.

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