

# What makes *Haloxylon persicum* grow on sand dunes while *H. ammodendron* grows on interdune lowlands: a proof from reciprocal transplant experiments

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**Abstract:** Determining the mechanisms underlying the spatial distribution of plant species is one of the central themes in biogeography and ecology. However, we are still far from gaining a full understanding of the autecological processes needed to unravel species distribution patterns. In the current study, by comparing seedling recruitment, seedling morphological performance and biomass allocation of two *Haloxylon* species, we try to identify the causes of the dune/interdune distribution pattern of these two species. Our results show the soil on the dune had less nutrients but was less saline than that of the interdune; with prolonged summer drought, soil water availability was lower on the dune than on the interdune. Both species had higher densities of seedlings at every stage of recruitment in their native habitat than the adjacent habitat. The contrasting different adaptation to nutrients, salinity and soil water conditions in the seedling recruitment stage strongly determined the distribution patterns of the two species on the dune/interdune. *Haloxylon persicum* on the dunes had lower total dry biomass, shoot and root dry biomass, but allocated a higher percentage of its biomass to roots and possessed a higher specific root length and specific root area by phenotypic traits specialization than that of *Haloxylon ammodendron* on the interdune. All of these allowed *H. persicum* to be more adapted to water stress and nutrient shortage. The differences in morphology and allocation facilitated the ability of these two species to persist in their own environments.

**Keywords:** *Haloxylon*; seedling recruitment; root distribution; biomass allocation; species distribution

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Spatial patterns of species diversity and species distribution are central to ecology and have fascinated naturalists, ecologists and biogeographers for centuries (Zimmermann et al., 2009; Eiserhardt et al., 2011). The factors influencing species distribution have become a major concern and attention has been focused on the roles played by climate (Honnay et al., 2002; Svenning and Skov, 2007), topography and habitat heterogeneity (John et al., 2007), dispersal (Svenning et al., 2008) and biotic interactions (Richards et al., 1997; Araújo and Luoto, 2007). However, determinants of species distributions vary on spatial and tem-

poral scales. For instance, climate appears to be important at the landscape level and above (Davis and Shaw, 2001; Walther et al., 2007). Soil or topography dominates at landscape and local scales, hydrology at local scales, and dispersal functions at all scales (Angert and Schemske, 2005). Therefore, understanding the mechanisms underlying the size, shape and dynamics of the geographic distributions of various species remains a key challenge (Pennisi, 2005; Gaston, 2009). Specifically, as the causes of species distributions do not function independently (McDowall, 2004) and are scale dependent (Levin, 1992), the importance

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of different mechanisms varies with scales (Hu et al., 2012; Schei et al., 2012).

At local (<1,000 m) to regional scales (100 km), Tuomisto and Poulsen (1996), Richards et al. (1997), and John et al. (2007) reported plant species' distributions are strongly associated with edaphic conditions including soil chemistry and nutrient availability. The influence of soil texture on hydrological conditions may affect plant species distributions and diversity (Rietkerk et al., 2002; Palm et al., 2007). Also, topography may affect plant distributions indirectly by modulating other environmental factors such as soil conditions, hydrology, wind exposure, as well as temperature and fog frequency (Svenning, 2001; Svenning et al., 2009). Although the influence of environmental conditions on plant distribution patterns have been well documented in the local scales, the related process and mechanisms causing these patterns are still poorly known, especially for tree species (Engelbrecht et al., 2007). Far less attention has been paid to the dominant processes and mechanisms mediating tree species distribution patterns during various life stages.

Among the main processes and mechanisms of population ecology, the regeneration stage is often the most critical stage during the life history of plants in determining adult plant distribution (Davis, 1991; Pratt et al., 2008), especially as it relates to adaptation to local edaphic and microclimatic conditions during germination and seedling establishment (Mustart and Cowling, 1993; Daws et al., 2002; Masaki et al., 2007). A reciprocal transplant approach had been considered to be an effective method to ascertain the importance of edaphic factors on seedling establishment and species distribution (Wang et al., 1997). By monitoring seedlings emergence, establishment, and mortality of species on their own and adjacent soils in natural habitats, the edaphic factors that determine the seedling distribution can be determined (Mustart and Cowling, 1993; Richards et al., 1997).

Furthermore, phenotypic plasticity, morphological characteristics and biomass allocation have long been proposed to be the key mechanisms used by plant species to adaptively maintain distributions by enhancing physiological and demographic components of fitness (Poot and Lambers, 2003; Pichancourt and van Klinken, 2012) and thus can also affect species distri-

bution (Pohlman et al., 2005; Pineda-García et al., 2011; Pichancourt and van Klinken, 2012). However, the role of morphologic traits and biomass allocation in influencing species geographic distributions has not yet been clarified in the field (Poot and Lambers 2003; Ellers and Stuefer, 2010).

*Haloxylon ammodendron* (C. A. Mey.) Bunge and *H. persicum* Bunge ex Boiss. et Buhse (Chenopodiaceae) are two xerophytic desert trees (Song et al., 2005). *H. ammodendron* occurs naturally in various habitats, including gravel desert, clay desert, fixed and semi-fixed sand, and saline land in Asian and African deserts (Tobe et al., 2000). *H. persicum* occurs naturally in non-saline sandy deserts in Central Asia, the Middle East, Afghanistan, northwestern China and Near Eastern deserts (Song et al., 2005; Al-Khalifah and Shanavaskhan, 2007). At the southern fringe of the Gurbantonggut Desert, the above two *Haloxylon* species are the major dominant species for their respective plant communities. *H. ammodendron* occupies interdunes and the flat slopes of dunes and *H. persicum* occurs mainly on the top of dunes, with both species rarely growing together. The contrasting distribution patterns of the two *Haloxylon* species have intrigued scientists in plant geography for many years. However, we are still far from fully understanding what controls this distribution pattern.

Sandy desert, characterized by the alternative distribution of sand dunes and interdune lowlands, usually shows a varying pattern of vegetation composition and contrasting plant community distribution on the dune and interdune habitats (Pemadasa et al., 1974; Avis and Lubke, 1996; Phillips et al., 2001; Liu et al., 2007). Desert dunes and interdune lowlands had been proven to provide habitat heterogeneity and to profoundly influence the spatial and temporal distribution of water and nutrients across the landscape (Rosenthal et al., 2005; Grigg et al., 2008; Zuo et al., 2009). Currently, topographic, edaphic and natural disturbance characteristics, such as the underground flow of saline water as well as sand movement or sand burial, influence species composition and distribution of dune ecosystems in deserts (Barnes and Harrison, 1982; Moreno-Casasola, 1988; Olff et al., 1993; Maun and Perumal, 1999). However, most of the research focused on coastal and lacustrine sand dune systems, making the results of such research barely applicable

to sand dune systems in the continental interior such as the Gurbantonggut Desert in Central Asia. Previous studies in this typical temperate desert showed soil mechanical composition significantly affects the vegetation distribution. *H. ammodendron* benefits from coarse textured soil along environmental gradients (Xu et al., 2006). For *H. ammodendron* growing on soils with contrasting textures, phenotypic plasticity in root properties may have evolved to help plants enhance resource capture (Xu and Li, 2008). Also, a study on the effects of sodium chloride (NaCl) on germination and growth of *H. ammodendron* and *H. persicum* seedlings in the laboratory indicated *H. ammodendron* had higher tolerance to salinity than *H. persicum* (Tobe et al., 2000; Song et al., 2006). Salinity tolerance during seed germination and the seedling stage may determine the geographical distribution of both species (Tobe et al., 2000; Song et al., 2005). However, such conclusions were mostly drawn from laboratorial experiments and whether they are applicable in natural field conditions remained unknown.

In the current study, we adopted a comparative approach to germination and seedling recruitment by reciprocal transplanting in the field; morphological traits and biomass allocation of the two species were studied in seedlings. The working hypotheses were: (1) differences in regeneration (seed germination and/or seedling establishment of the two species) in a dune/interdune system determine the typical dune/interdune distribution of the adult trees; and (2) to adapt to different habitats, both species develop habitat specialization basing on their morphology and resource allocation patterns.

## 1 Materials and methods

### 1.1 Habitat and species

The field experiments were conducted during two growing seasons, during May to October 2009 and 2010, in their native habitats at the southern fringe of the Gurbantonggut Desert in the vicinity of the Fukang National Field Scientific Observation and Research Station for Desert Ecosystems (44°17'N, 87°56'E; 475 m asl). Typically, this region has a temperate, continental, arid climate, with dry, hot summers and cold winters. Annual precipitation is between 70 and 180 mm and annual pan evaporation is 10 times greater than annual precipitation. A site was selected for the experimental area far from human influence and in-

cluding above two *Haloxylon* species with typical sand dunes-interdune lowlands distribution. Basing on a field survey from 5 sites, the mean density of adult trees was 120 plants/hm<sup>2</sup> for *H. persicum* and 700 plants/hm<sup>2</sup> for *H. ammodendron* in their respective habitats.

### 1.2 Background data: soil physical and chemical properties

Soil particle sizes were measured with a Malvern Laser Analyzer in the laboratory on soil samples of respective habitats from the experiment site. Bulk densities and degree of porosity were determined by conventional methods using a ring sampler. Stable infiltration rates were measured by a double-ring infiltrometer. The locations for sampling and measurements were randomly selection and carried out on top soil in each habitat with five replicates.

In each habitat, about 2 kg of dry soil was collected from 0 to 10 cm according to the germination depth and placed inside a paper-lined calico bag. The mixed soil samples were air-dried in a ventilated room and hand-sieved through 0.25-mm mesh to remove roots and other organic debris. After the pretreatment, the mixed soil samples in each habitat were subsampled each with five replicates for the following analyses. Soil pH and electrical conductivity (EC) were measured in a soil-water suspension (1:5 soil:water ratio; Li et al., 2011). Soil organic carbon (SOC) was measured by the K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub>-H<sub>2</sub>SO<sub>4</sub> oxidation method of Walkley-Black (Nelson and Sommers, 1982). Total soil N (TN) was measured by the Kjeldahl procedure (UDK140 Automatic Steam Distilling Unit, Automatic Titroline 96, Italy). Total soil P (TP) and K (TK) were measured with the Mo-Sb antispectrophotography method using a spectrophotometer (UV-2401PC, Japan); concentrations of PO<sub>4</sub><sup>3-</sup>, NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, K<sup>+</sup>, Na<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup>, Cl<sup>-</sup> and SO<sub>4</sub><sup>2-</sup> were determined using a capillary electrophoresis system, while CO<sub>3</sub><sup>2-</sup> and HCO<sub>3</sub><sup>-</sup> were determined by titration with 0.1 mol/L HCl until the sample pH reached 4.3 (Patnaik, 1997).

The soil water content was measured within the profiles to 2-m at 0.1-m intervals, in the two habitats over the peak growing season from June to September 2010. Soil samples were extracted by an auger with three replicates at each depth every 5 days from three different randomly selected locations in each habitat. The samples were then stored in aluminum boxes and dried at 105°C to constant weight. To monitor the soil

water content variation in the soil profile induced by the snow-melt in early spring, we measured the soil water content at 0.1-m intervals from soil surface to the depth of 3 m. The measurement was started on 28 March when the snow melting started and continued until the upper dry layer appeared on 25 April 2010, with three replicates at each depth.

Pressure membrane tests were conducted on the soil in the two habitats to determine the equilibrium water content retained in a soil subjected to pressures of  $-0.1$ ,  $-0.2$ ,  $-0.5$ ,  $-1.0$ ,  $-1.2$  and  $-1.5$  MPa in each plot. The data was used to obtain soil water release curves by fitting of the van Genuchten model (van Genuchten, 1980). We then used the curve fitted for each plot to calculate the soil matrix water potential basing on soil water content.

### 1.3 Experiment 1: reciprocal seed transplants in the field

We collected seeds near the study area in late October 2009, the year before conducting our seed planting experiment. We planted seeds at a depth of 5 mm in reciprocal transplants on 23 March 2010 before snow melt. At the sand dune and interdune lowland, 20 plots were seeded for each species with 10 plots on the dune and 10 plots on the interdune lowland randomly selected. The horizontal distance between the plots grouping on the dune/interdune was about 50 m, totally there were 40 plots and each plot area was  $1\text{ m} \times 1\text{ m}$ . In each plot, we planted 400 seeds in rows with the seeds 5 cm apart. We recorded the number of emerging seeds at 3-day intervals and checked survival at about 1 week intervals until the middle of September.

### 1.4 Experiment 2: investigation of specific adaptation in biomass allocation and morphology to their native habitats

Five 1-year-old seedlings of each species from their natural habitat plots were chosen for excavation from their respective home plots on 20 September 2010 following the details provided by Xu and Li (2006) as described below. Tree height, basal stem diameter and canopy width were measured prior to excavation. A 1-m diameter ring ditch for the 1-year seedlings was dug around each target plant to uproot it. The huge cylinder of soil containing the rhizosphere was thus isolated, then rinsed off followed by the soil being removed by hand to expose the roots. The diameter and length of lateral root segments were measured

with a ruler and caliper. Detailed excavation and root surface area measurement methods have been reported previously (Xu and Li, 2006). After investigation of root distribution the sampled trees were partitioned into below and above ground parts. The above ground parts were subdivided into foliage and woody parts. Specifically, a small fraction of roots with diameters  $<2$  mm were separated and measured for length and diameter with vernier caliper and ruler, which was used to calculate root length per dry mass (specific root length, SRL) and root surface area per dry mass (specific root area, SRA). All the parts were oven-dried at  $65^{\circ}\text{C}$  to a constant weight and the dry biomass was measured using an electric balance.

About 10 g of new, fully expanded leaves were collected from five individuals of each species during June 2010. Fresh leaf area was determined with a scanner in the laboratory. Leaves were oven-dried at  $65^{\circ}\text{C}$  to a constant weight and dry mass was measured. We calculated specific leaf area (SLA) basing on leaf area per unit of leaf dry mass. We calculated leaf surface areas of entire trees basing on dry biomass of foliage and SLA.

### 1.5 Data analysis

Descriptive statistics were used to calculate mean values and standard errors of the mean for each data set. Mean values of soil physical/chemical properties and morphological parameters for the two sites and species were compared with Student's *t*-tests. Charting was done with Origin 8.0 software (OriginLab Corp., Northampton, MA, USA).

## 2 Results

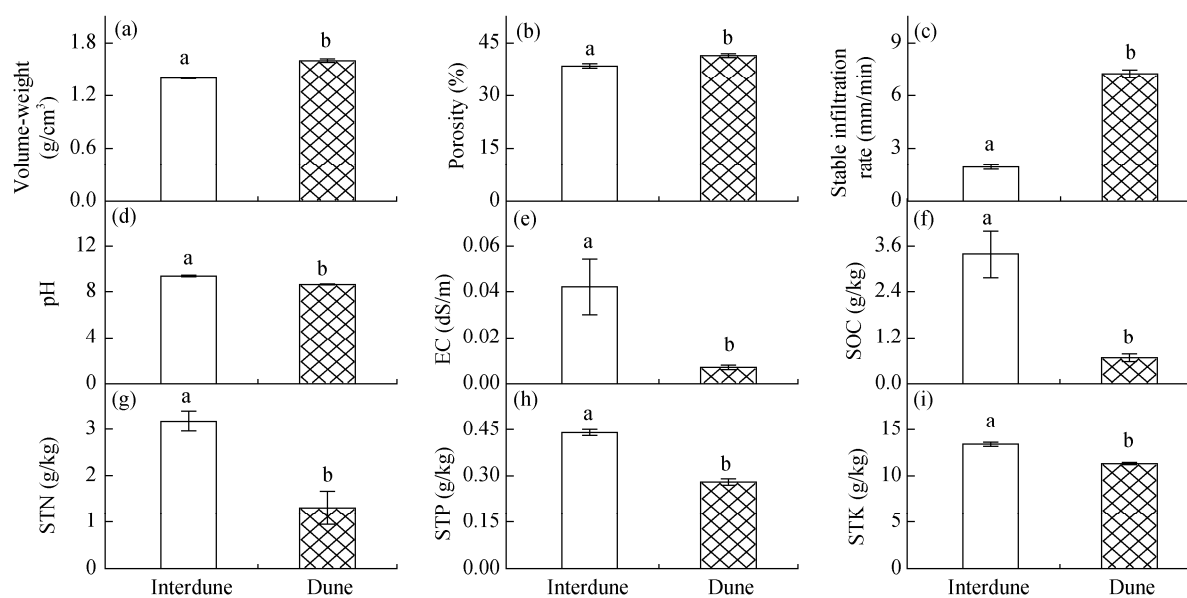
### 2.1 Soil physical, chemical and hydraulic properties

The soil particle sizes were  $<2,000\text{ }\mu\text{m}$ . The soil on the interdune lowland consisted of 1.3% clay, 13.7% loam and 85% sand; the soil on the sand dune consisted of 0.3% clay, 3.8% loam and 96.2% sand. Figures 1a, b and c show the soil physical properties at the two sites. Bulk density was significantly higher ( $P<0.01$ ) on the top of the dune ( $1.6\pm0.02\text{ g/cm}^3$ ) than in the interdune ( $1.4\pm0.01\text{ g/cm}^3$ ). The degree of porosity (ratio by volume) was  $41.41\pm0.56$  on the dune and was significantly different at  $38.49\pm0.63$  on the interdune ( $P<0.01$ ). The stable infiltration rate was  $7.24\pm0.23\text{ mm/min}$  on the dune and significantly different at  $1.93\pm0.13\text{ mm/min}$  on the interdune

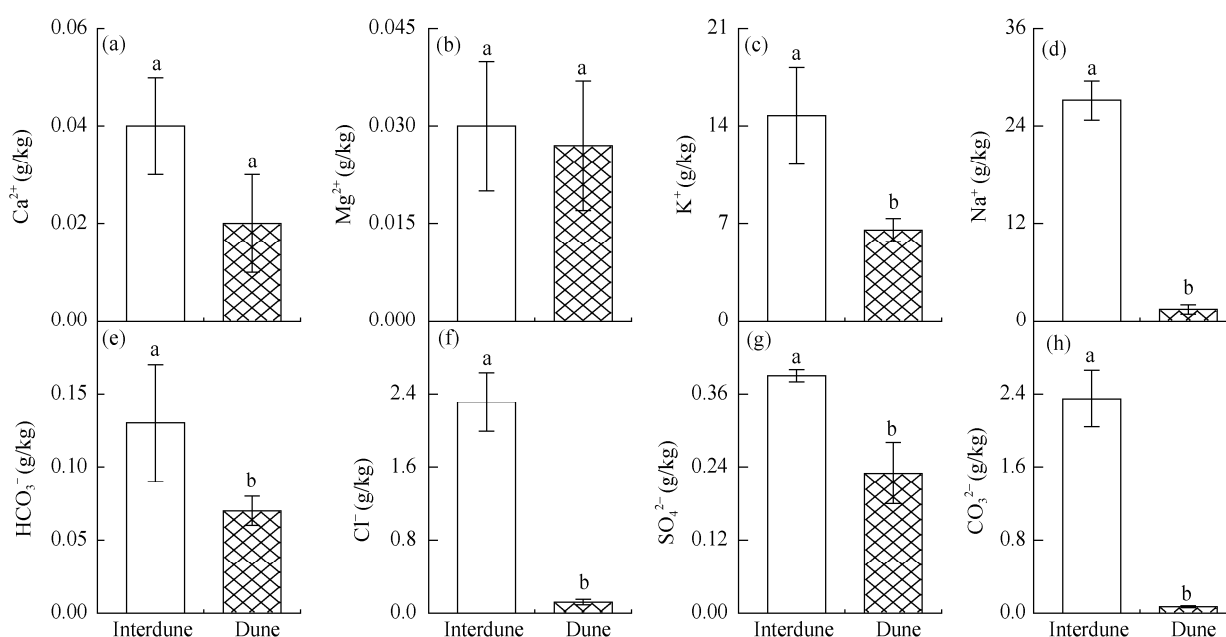
( $P < 0.001$ ). Soil pH, electrical conductivity (EC), soil organic carbon (SOC), soil total N (STN), soil total P (STP) and soil total K (STK) were higher on the interdune than on the dunes (Figs. 1d–i). Soil soluble ion concentrations of  $K^+$ ,  $Na^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$ ,  $Cl^-$ ,  $CO_3^{2-}$ ,  $HCO_3^-$  and  $SO_4^{2-}$  were also higher on the interdune than on the dunes (Fig. 2) which indicated the soil on

the dune had less nutrients but was less saline than that of the interdune.

Figures 3 shows the average of soil moisture and corresponding soil water potential in each soil layer during the growing season and just after snow melt. On average, except in the upper soil layers (0–40 cm), soil moisture content in each layer on the dune was

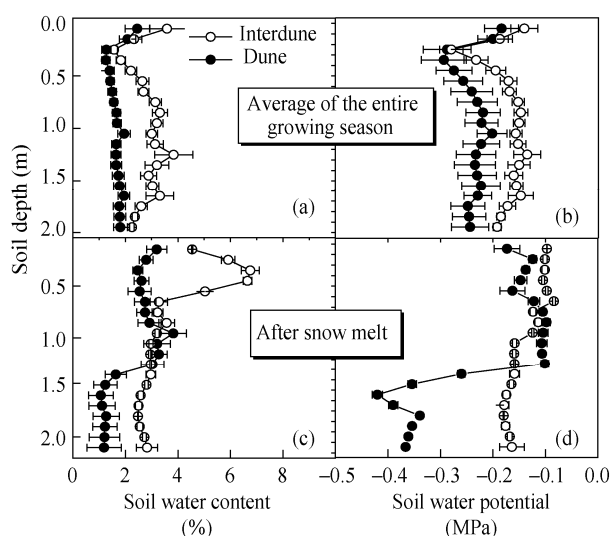


**Fig. 1** Soil physical (a–c) and chemical properties (d–e) and nutrient contents (f–i) at two sites. Values in the same panel labeled with different letters are significantly different at  $P < 0.05$ . Mean  $\pm$  SE,  $n = 5$ . EC, soil electrical conductivity; SOC, soil organic carbon; STN, soil total N; STP, soil total P; STK, soil total K.



**Fig. 2** Soil soluble ion content in two habitats. Values in the same panel labeled with different letters are significantly different at  $P < 0.05$ . Mean  $\pm$  SE,  $n = 5$ .

lower than that of the interdune; the average soil water content within the soil profile during the entire growing season was 1.87% on the dune compared to 2.80% on the interdune ( $P < 0.001$ ; Fig. 3a). Figure 3c shows soil water content within the soil profile after snow melt. The maximum infiltration depth after snow melt was 1.6 m on the dune and 0.9 m on the interdune which was consistent with a stable infiltration rate in the two experiment plots (Fig. 1c). Figures 3b and d give the average of soil water potential in each soil layer during the growing season and after snow melt, respectively. On average, except in the upper soil layers (0–40 cm), soil water potential in each layer on the dune was non-significantly lower than that of the interdune; the average soil water potential within the soil profile of the entire growing season was  $-0.24$  MPa on the dune compared to  $-0.17$  MPa on the interdune ( $P > 0.05$ ; Fig. 3b). However, the difference was significant during summer drought. In late June 2010, at the beginning of the summer drought period, a soil water potential below  $-1.5$  MPa occurred on the interdune from the soil surface to the soil depth of 0.4 m. But this did not occur on the dune at the same period. In the extreme drought period (mid September) on the dunes, soil water potential was below  $-1.5$  MPa



**Fig. 3** Soil water content and soil water potential down the soil profile: (a) average soil water content during the peak growing season from June to September 2010; mean $\pm$ SE; (b) corresponding average soil water potential at each depth; mean $\pm$ SE; (c) soil water content at each depth immediately after snow melt; (d) corresponding soil water potential at each depth after snow melt.

from the soil surface to the depth of 1.6 m, but on the interdune, the same occurred from the soil surface to the depth of only 0.5 m.

## 2.2 Seedling emergence and survival

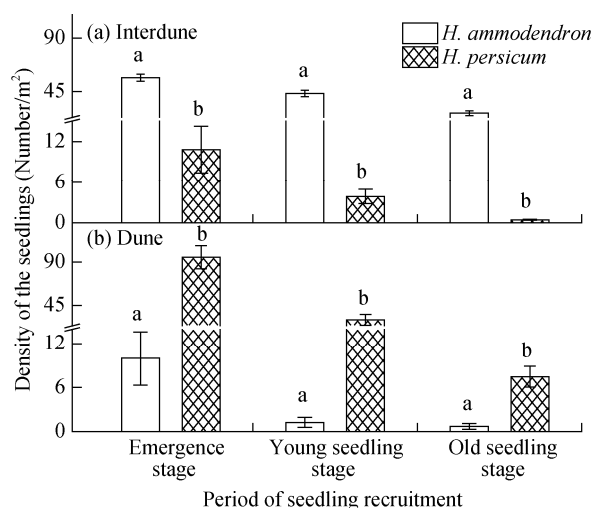
Seedlings began to emerge 45 days after being planted on 23 March 2010. Most seedlings emerged from middle to late April. At the same habitat emergence was significantly higher for the native species than the foreign species. For the same species there was also significantly higher emergence on its native habitat than on the adjacent one. High seedlings mortality appeared at the beginning of May and lasted to early June. For the same species there were more seedling deaths on the exchange habitat than their native habitat. In the same habitat, there was more seedling survival for the native species than the foreign species. Compared with their native habitats, very few individuals had survived on the exchange habitat at the end of the growing season (Fig. 4).

## 2.4 Biomass allocation and morphological traits

The 1-year-old seedlings of *H. ammodendron* had higher total biomass, root dry mass, shoot dry mass but a lower root:shoot dry mass ratio and root:leaf surface area ratio than *H. persicum* (Fig. 5). Compared to *H. ammodendron*, *H. persicum* invested more photosynthate to belowground resources as the root:shoot biomass ratio indicated. Root depth was shallower for *H. ammodendron* than that of *H. persicum* for the 1-year old seedlings (Fig. 5). The distribution of surface area of lateral root was shown in Fig. 6. The lateral root surface area of *H. ammodendron* was higher than that of *H. persicum*. The results of investigation of morphological traits showed *H. ammodendron* had higher specific leaf area and smaller specific root length and specific root area than that of *H. persicum* (Fig. 7).

## 3 Discussion and conclusion

The most ecologically relevant biological aspects investigated were seedling recruitment, phenotypic trait performances (morphological traits) and biomass allocation. We emphasize the importance of the impact of soil factors on seedling recruitment in determining the current typical habitat distribution. Selection favored the more water stress tolerant and nutrient shortage

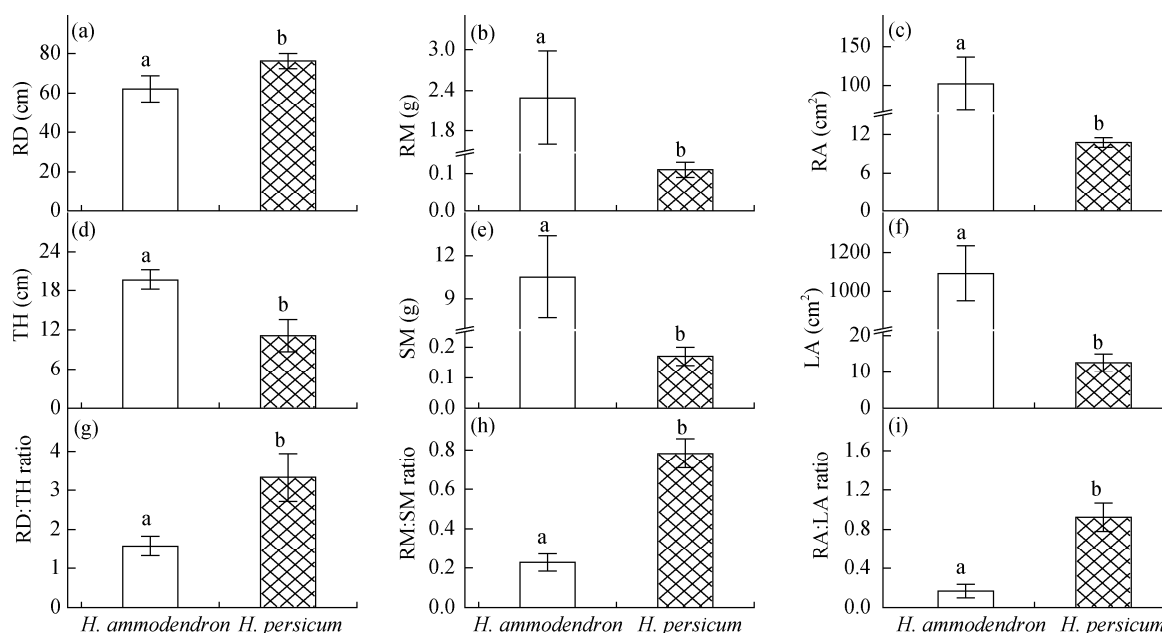


**Fig. 4** Change of the density of *H. ammodendron* and *H. persicum* seedlings in interdune lowlands (a) and sand dunes (b) in their natural habitats and foreign habitats under field conditions in 2010. The emergence stage was from 15 to 30 April; the number of the seedlings of each species in 10 plots (1-m<sup>2</sup> for each plot) was counted five times at 3 day intervals and then averaged, so the value was the mean $\pm$ SE with 50 replicates during germination. The young seedling stage was from 1 May to 15 June, the observations were conducted eight times with a 6–7 day intervals and the value was the mean $\pm$ SE with 80 replicates. The older seedling stage was from 15 June to 14 September, counting was conducted 15 times with 6–7 day intervals and the value was mean $\pm$ SE with 150 replicates. Values in the same panel labeled with different letters are significantly different at  $P < 0.05$ .

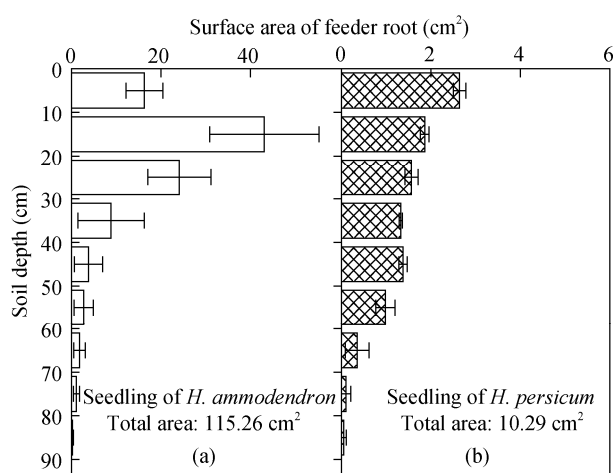
adapted *H. persicum*'s occupation of the top dunes and the more salinity adapted *H. ammodendron*'s occupation of the lowland between the dunes.

### 3.1 Determinants of dune-interdune species distribution

We used reciprocal transplants to evaluate the influence of soil factors on seedling recruitment and the importance of those factors to the dune-interdune species distribution. The two species studied here had much lower seedling densities when planted on soil substrates where they did not normally occupy than when planted on their normal soil substrates during the recruitment stage (Fig. 4). Seedling performance and survival of species was better on its own soil type rather than on the exchange soil type. These results indicate soil factors affected seedling emergence and establishment. Because of the higher soil salinity between the sand dunes (Figs. 1 and 2) and lower seed germination and seedling survival on the higher NaCl concentrations in the laboratory (Song et al., 2005, 2006), we can conclude soil salinity constrains *H. persicum* distribution on the lowland between the dunes.



**Fig. 5** One-year-old seedling rooting depth:tree height ratio (a, d, e), biomass allocation pattern (b, e, h) and root to leaf area ratio (c, f, i). Different letters in the same panel indicate significant differences at  $P < 0.05$ . Mean $\pm$ SE,  $n=5$ . RD, rooting depth; TH, tree height; RM, root dry biomass; SM, shoot dry biomass; RA, lateral root surface area; LA, leaf surface area.



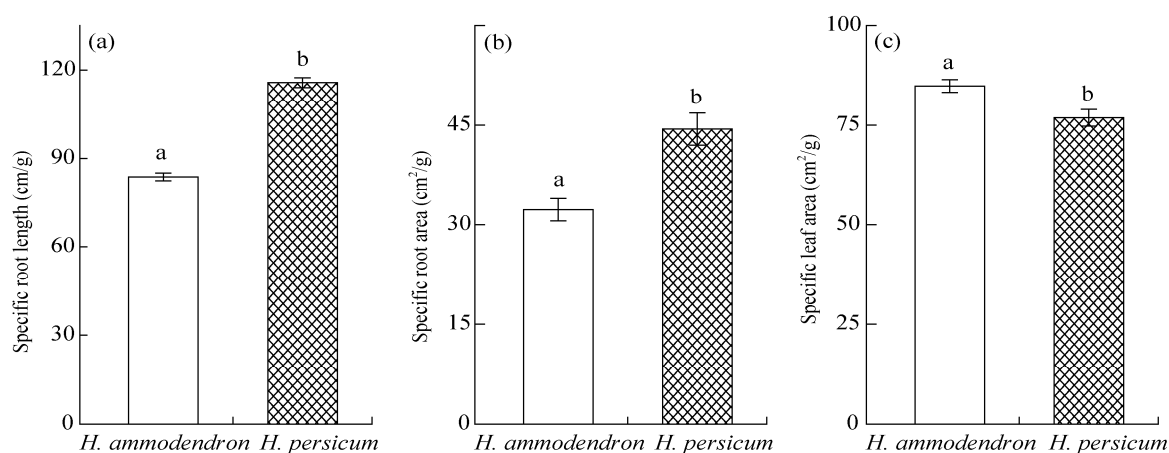
**Fig. 6** Distribution of the surface area of the lateral roots in the soil profile at 10-cm depth intervals. One-year-old seedlings of *H. ammodendron* and *H. persicum* were excavated in the experimental plots on interdune lowlands (a) and the top of sand dunes (b). Mean $\pm$ SE,  $n=5$ .

Padilla and Pugnaire (2007) reported maximum root depth is important for species survival during periods of drought. Drought in desert ecosystems was also closely related to plant distribution (Barnes and Harrison, 1982; Groom, 2004). For *H. ammodendron*, low soil salinity in the dune may partially constrain seedling survival as reported by Tobe (2000): a hydroponic culture of *H. ammodendron* over around 3 months with NaCl solutions of 0, 200, 400 and 600 mmol/kg showed that the survival was highest (82.3%) at 400 mmol/kg NaCl. Also, the slower root vertical extension speed of *H. ammodendron* compared to that of *H. persicum* in the seedling stage (Fig. 7a) may lead to the higher seedling mortality on the dunes. The higher mortality of *H.*

*ammodendron* on the dunes may be aggravated by lower water availability in the dunes than occurs in their natural interdune habitat (Fig. 3). Habitat heterogeneity in soil water and salinity resulted in strong selection pressures on germinating seedlings. The differing adaptability of these two species to salinity and soil water conditions during the recruitment stage eventually determines adult distribution patterns. Therefore, the contrasting germination and survival requirements between the two species in their recruitment stage lead to preferential germination and seedling emergence on its native soil substrate. Our findings support the hypothesis that differences in regeneration in a dune/interdune system determine the typical dune/interdune distribution of the adult trees.

### 3.2 Advantages of the two *Haloxylon* species in their own environments

The trade-off in allocation patterns and phenotypic traits is important for maintaining a plant's adaptation to environmental limiting factors (Kitajima, 1994; Cornelissen et al., 1996) and is closely related to species distribution (Poot and Lambers, 2003, 2008). *H. Persicum* with a smaller stature (smaller total biomass) invested a larger allocation of biomass to roots, maintained a larger root/shoot ratio (Figs. 5 b–i) and larger specific root length (Fig. 7a) and specific root area (Fig. 7b). All of these make *H. persicum* more adapted than *H. ammodendron* to water stress and nutrient shortage in a water- and nutrient-limited environment. These results were consistent with our second work hypothesis. A comparison between rare and common



**Fig. 7** Lateral root and leaf morphological characteristics of the two *Haloxylon* species: (a) specific root length; (b) specific root area and (c) specific leaf area. Different letters in the same panel indicate significant differences at  $P<0.05$ . Mean $\pm$ SE,  $n=3$ .



species by Poot and Lambers (2003) showed the trade-off in whole plant biomass allocation (investment in root or shoot) and within root biomass allocation (high or low specific root length) may cause them to be well adapted to their own environment, but poorly adapted to others. However, root:shoot ratio is obviously not static, but changes with plant size, and may have to be followed over a longer period for differences to be observed. Additionally, total root length is a better predictor of explorable soil volume and, therefore, of the capacity of roots to absorb nutrients and water than absolute root mass. Furthermore, competition between congeneric species in the boundary zone is frequently more intense than between unrelated species (Walck et al., 2001; Milla et al., 2011) and responsible for the large differences in these two species' geographical distributions and habitats (Theodose and Bowman, 1997; McGill, 2010). Therefore, the role of the competition in the two species' spatial distribution pattern should receive more attention.

The results from our study indicated the two species adapt to salinity and soil water conditions differently during the germination and seedling establishment stages and this strongly determined the distribution patterns of the two species. Both species had higher densities of seedlings at every stage of recruitment in their native habitat than the adjacent habitat. *H. persicum* on the dunes had lower total dry biomass, shoot and root dry biomass, but allocated a higher percentage of its biomass to roots and possessed a higher specific root length and specific root area by phenotypic traits specialization than that of *H. ammodendron* on the interdune. The differences in morphology and allocation facilitated the ability of these two species to persist in their own environments. Selection favored the higher drought tolerant and barren adapted *H. persicum*'s occupation of the dunes and the higher salinity adapted *H. ammodendron*'s occupation of the lowland between the dunes.

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