

# Growth stages affect species richness and vegetation patterns of nebkhas in the desert steppes of China



Weicheng Luo, Wenzhi Zhao \*, Bing Liu

Linze Inland River Basin Research Station, Key Laboratory of Inland River Basin Ecohydrology, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou, China

## ARTICLE INFO

### Article history:

Received 25 February 2015

Received in revised form 16 September 2015

Accepted 19 September 2015

Available online xxxx

### Keywords:

Desert steppes

Nebkha growth stage

Nebkha morphology

Species composition

Species growth form

## ABSTRACT

Nebkhas are important indicators of land degradation in desert steppes and play an important role in the ecological and evolutionary dynamics of desert steppe ecosystems. This study examined the relationship between the diversity of plant species and nebkha morphology during different growth stages of the nebkhas. In this study, each nebkha is defined as a self-contained unit. The species composition and vegetation patterns within each unit during different stages of formation were investigated, while also the plant species within the inter-nebkha area of the desert steppe field were examined. Results show that more than 90% of the species within the nebkha units were herbaceous. In developing nebkhas, the increase in nebkha size was associated with an increase in the herb species richness but a decrease in the overall plant density. When nebkha size was constant, similar correlations with species richness or density were found. The richness of species within the inter-nebkha area was significantly higher compared to developing nebkhas during periods of growth, but lower when nebkha development was complete and growth had stalled. The density of species was significantly higher in the nebkhas than the inter-nebkha area during all developmental periods. Thus, nebkhas provide a highly favorable condition for plant recruitment and survival when fully developed. However, when nebkhas are still forming, the inter-nebkha areas provide greater plant support. These results have important implications to biodiversity conservation in desert steppe fields.

© 2015 Published by Elsevier B.V.

## 1. Introduction

Phytogenic nebkhas, often referred to as coppices (Link et al., 1994; Rango et al., 2000; Wood et al., 1978) or vegetated dunes (Nishimori and Tanaka, 2001; Wang et al., 2008), are mounds of wind-borne sediment associated with the canopies of plants (Batanouny, 2001; Tengberg and Chen, 1998; Vasek and Lund, 1980). They are commonly distributed in arid, semi-arid, and sub-humid regions (Nickling and Wolfe, 1994; Parsons et al., 2003), and their formation is determined by several factors. These factors include: climate change, vegetation degradation, anthropogenic activity and the hydrogeological condition of the local area (Cabrera-Vega et al., 2013; Tengberg, 1995; Yan et al., 2005; Wang et al., 2006). Plant type and sand conditions strongly influence the morphological characteristics of developing nebkhas (El-Bana et al., 2007; Khalaf et al., 1995).

In desert steppe ecosystems, nebkhas are important indicators of land degradation (Cabrera-Vega et al., 2013; Wang et al., 2006). Nebkhas work to combat land degradation by stabilizing soil surfaces, preventing soil erosion and facilitating plant recruitment and survival

(Aguilar and Sala, 1999; Brown and Porembski, 1997; Titus et al., 2002; El-Bana et al., 2002). Hence, the stability of the desert steppe ecosystem may be highly dependent upon the formation of nebkhas and their promotion of biodiversity conservation and vegetation restoration (El-Bana et al., 2003). Thus, the development of nebkhas is an important ecological consideration in the environmental studies of desert steppes (El-Bana et al., 2002; Okin, 2013).

The spatial distribution of resources, like soil moisture or nutrients, within the nebkhas is different from those in the surrounding area (El-Bana et al., 2003; Hesp and McLachlan, 2000). Nebkhas contain highly heterogeneous distributions of perennial biomasses (Okin, 2013) and are fertile islands in comparison to the barren land surrounding them (Carrera et al., 2003; Schlesinger et al., 1996; Stock et al., 1999). This is particularly notable in un-grazed land, where species richness and abundance are particularly higher in nebkhas compared to the inter-nebkha area (El-Bana et al., 2003). In conjunction with a poorer soil composition, soil temperature and photosynthetically active radiation are highest in the inter-nebkha area (Domingo et al., 2000), making the conditions within nebkhas more favorable for plant growth. Importantly though, the favorable conditions in the nebkhas are dependent on the surrounding environment since a reduction in vegetation cover between them could cause serious wind and water erosion to the nebkhas (El-Bana et al., 2003).

\* Corresponding author.

E-mail address: [zhaowzh@lzb.ac.cn](mailto:zhaowzh@lzb.ac.cn) (W. Zhao).

The positive effect of nebkhas on plant abundance and richness within the desert steppe is dependent on nebkha morphology (El-Bana et al., 2003). Plant species richness is significantly related to nebkha size by a single-power function, as predicted by the island biogeography theory. The nature of this relationship within nebkhas is dependent on the identity of the nebkha's host species, since the host species can affect the growth and survival of other species (El-Bana et al., 2003, 2007; Pool et al., 2013). It is known that the interaction between species can significantly affect the species structure and the composition of communities and ecosystems in either a positive or negative manner (Brooker, 2006; Gao et al., 2014; le Roux et al., 2013; Holzapfel and Mahall, 1999; Schenk and Mahall, 2002). For example, relatively larger annual plant species can support the growth of smaller annuals, like shrub nurse-plants (Armas and Pugnaire, 2005). By contrast, the influx of alien species can negatively influence the existing plant community, and cause a reduction in diversity and loss of native species (Levine et al., 2003).

The relationship between the number of species and the area sampled is one of the oldest and best-documented patterns in community ecology (He et al., 2005). However, this relationship differs greatly among desert, grassland and woodland areas (Crawley and Harral, 2001; He et al., 2005). Most documentation of these relationships is on coastal or desert systems, while little information is available for desert steppe systems. Even fewer studies have examined the species richness and composition within developing nebkhas or inter-nebkha area in desert steppe fields. Therefore, the aim of this study was to: (1) examine the relationship between plant speciation and nebkha morphology; (2) identify possible vegetation differences between the nebkha and

the inter-nebkha area; and (3) determine whether the stage of nebkha development affects the degree of speciation within the nebkhas. To do this, we studied the patterns of species richness and composition within nebkhas formed by *Nitraria tangutorum* and the surrounding inter-nebkha area in the desert steppes of China.

## 2. Materials and methods

### 2.1. Study site

The study site was located in a desert steppe field south of Mu Us Sand land (37° 04'–38° 10' N, 106° 03'–107° 47' E, 1354 m a.s.l.), in Ningxia, China (Fig. 1). The region typically has a typical temperate continental climate. The annual mean temperature is 9.2 °C. The average annual rainfall is 280 mm, primarily accumulating during the summer and autumn seasons, and the average amount of evaporation totals 2100 mm per year (Zhou et al., 2015). The growing season starts in late April and ends in late September. Grasslands and sandy banks are largely distributed throughout this area, constituting of about 64% and 23% of the total area, respectively. In contrast, forests occupy only 11% of the land area, and croplands make up 2% (Liu et al., 2010). The windy season is from March until May. Wind has significant impacts on the natural environment of this area, and is one of the most prevalent causes of desertification. The prevailing wind directions are westerly and northwesterly, and the average wind speed is about 2.8 m per second (Shen, 2008). The main soil types of this area are aeolian sandy soil and loessial soil. The average nutrient content of the soil in the central



Fig. 1. Location of the study area (Zhou et al., 2015).

and northern regions of this area is as follows: organic matter, 6.60 g/kg; hydrolysable nitrogen, 27.15 mg/kg; available phosphorus, 4.26 mg/kg, and vegetation coverage was 30% (Shen, 2008).

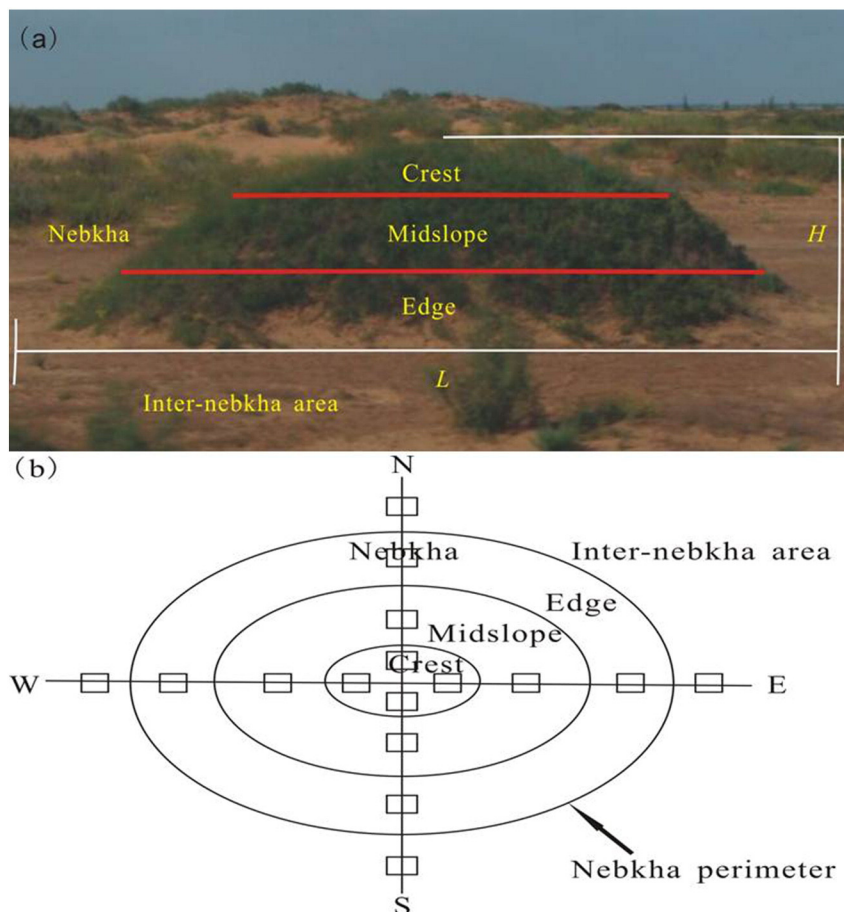
## 2.2. Field sampling

*Nitraria tangutorum* is the host species within many nebkhas distributed across the Gobi Desert and along the periphery of oases in arid Northwest China. This species plays an important role in fixing and binding mobile sand. It is also characterized by a significant drought and salt tolerance, and an ability to produce offspring through clonal propagation when its stems are buried under sand (Su et al., 2012). *N. tangutorum* is effective in trapping wind-laden sediments and often forms nebkhas in the oasis-desert ecotone in Northwest China. The protection of the *N. tangutorum* formed nebkhas is important for desertification control and oasis maintenance in the oasis-desert ecotone (Su et al., 2006).

Sampling was carried out in July 2013. In the field investigation, we selected four large plots (200 m × 200 m) in the desert steppes. Defining each *N. tangutorum* formed nebkha as a self-contained unit we selected 100 widely spaced nebkhas, both large and small, in each plot. Each nebkha was independent of any neighboring nebkhas so that the distance between neighboring nebkhas was no more than 5 m and completely isolated from neighboring nebkhas to avoid the inter-nebkha effects (El-Bana et al., 2002, 2003). In total, the study examined 397 nebkhas. Each nebkha was measured and the length ( $L$ ) and width ( $W$ ) were used to calculate the area for each one (Fig. 2a).

We defined three size classes of nebkhas based on our morphometric measurements, in particular the height of the nebkha dunes ( $H$ ) (Table 1): small nebkhas ( $H < 1.0$  m), medium nebkhas ( $1.0 \text{ m} \leq H < 2.0$  m) and large nebkhas ( $H \geq 2.0$  m). Small and medium nebkhas represented those in growing stage, while large nebkhas were indicative of complete development and no longer changing in size and in stabilizing stage (Tengberg and Chen, 1998; Zhang et al., 2011). For small and medium nebkhas, we recorded the species composition and abundance over the entire nebkha. Six  $1 \text{ m} \times 1 \text{ m}$  quadrats adjacent to each nebkha were selected to examine the species within the inter-nebkha areas. For analysis of the large nebkhas, we divided each nebkha into four parts (Fig. 2a): the inter-nebkha area (about 1 m away from the nebkha perimeter with microtopography), the nebkha edge (from nebkha edge to  $1/3 H$ ), the nebkha midslope (from  $1/3 H$  to  $2/3 H$ ) and the nebkha crest (from  $2/3 H$  to  $1 H$ ). For each nebkha, transects were placed at the nebkha crest and radiated out to the inter-nebkha area in the four cardinal directions (east, west, south and north) (Fig. 2b). Four  $1 \text{ m} \times 1 \text{ m}$  quadrats were then selected in each direction, three on the nebkha and one in the inter-nebkha area. We then recorded the plant species present and the individual densities for each species within each quadrant. The functional groups of species were defined according to (TCSIMNAR) (1985). For bunchgrasses, we counted the number of clusters to determine the density but for species with discrete individuals, we counted the number of individuals (Liu et al., 2007).

We also measured the soil moisture within the nebkhas and inter-nebkha areas 15 days after the last rain of the season. We randomly choose 20 nebkhas of different sizes and sampled the soil for water



**Fig. 2.** (a) Sand fixation function of *N. tangutorum* nebkha mounds with the four identified parts (nebkha crest, nebkha midslope, nebkha edge and inter-nebkha area) of each nebkha;  $L$ , nebkha length;  $H$ , nebkha height. (b) Principle scheme of sampling design on the nebkha mound with  $1 \text{ m} \times 1 \text{ m}$  quadrats lay along the four cardinal directions (El-Bana et al., 2002).

**Table 1**  
Size of nebkhas in the study area selected for sampling.

	Small	Medium	Large
Nebkhas height (m)	0–1	1–2	>2
Nebkhas area (m <sup>2</sup> )	0–30	30–50	>50
Nebkhas volume (m <sup>3</sup> )	0–20	20–50	>50

content in both nebkha and inter-nebkha areas. Soil samples were collected from depths of 0 m to 1.0 m, with every 0.1 m of depth defined as a different layer. Soil samples were oven-dried (105 °C) for 48 h prior to analysis.

2.3. Data analysis

Nebkha size was calculated as an elliptical area ( $[\pi(L \times W)/4]$ ), and nebkha volume was calculated as a hemi-ellipsoid ( $\pi(L \times W \times H)/6$ ) (Zhang et al., 2011). Regression analysis was used to determine the relationships between plant richness and nebkha area (El-Bana et al., 2002). The areas of the nebkhas were independent variables. Statistics were performed using the SPSS 18.0 software package (SPSS, Chicago, IL, USA).

The density of species was defined as the number of each species per m<sup>2</sup> in all quadrats (Liu et al., 2007). The species richness was defined as the total species numbers of each quadrat (Magurran, 2004). Statistical significance was determined with one-way ANOVA analysis. The post hoc LSD's test was used to distinguish functional groups of species in different sizes of nebkhas and Tukey's student *t*-test was used to compare nebkha and inter-nebkha area. Differences greater than  $p = 0.05$  were determined to be significant.

3. Results

3.1. Characteristics of nebkhas and species composition

The height of *N. tangutorum* within the nebkhas ranged from 0.2 m to 4.8 m, with the majority (90.1%) standing between 0.2 m and 3.0 m

tall (Fig. 3). The volumes of the nebkhas varied from 0.11 m<sup>3</sup> to 805.17 m<sup>3</sup>, with the majority (63.3%) between 0.11 m<sup>3</sup> and 50.0 m<sup>3</sup>. Notably, only 6.1% had a greater volume than 150 m<sup>3</sup>. The areas of the individual nebkhas varied from 0.86 m<sup>2</sup> to 333.3 m<sup>2</sup>. No less than 72.3% of them were smaller than 50 m<sup>2</sup>, and only 3.0% were larger than 100 m<sup>2</sup>. We found 45 plant species distributed across 397 nebkhas: 93.3% were herbs (46.7% were annual herbs, 6.6% were annual-biennial herbs and 40.0% were perennial herbs), while 6.7% were shrubs. These belonged to 11 different families but 66.7% of the species were *Compositae*, *Chenopodiaceae* or *Gramineae*. Similar to the speciation in nebkhas, there were 49 types of plants in the inter-nebkha area and nearly 91.8% of them were herbs (42.9% annual, 6.1% annual-biennial and 42.9% perennial) (Table 2). All 45 species found in the nebkhas were subsets of the 49 species found in the inter-nebkha areas.

Soil water content (at the depth of 0 m to 1.0 m) in the inter-nebkha areas was significantly higher than in the nebkhas. The soil water content in the inter-nebkha areas increased as soil depth increased (Fig. 4).

3.2. Species richness in nebkhas and adjacent habitat

The main herbal vegetation in the desert steppe included *Salsola collina* Pall., *Bassia dasyphylla* Kuntze, and *Chloris virgata* Sw. The shrubs included *Artemisia ordosica* Krasch, *Salix gordejvii* and *N. tangutorum*. The complete collection of species found in this study is listed in Appendix A.

The species richness and density within the nebkhas were significantly different than those found in the inter-nebkha areas during different stages of nebkha formation. During early nebkha growth stages the richness of species, such as annual herbs ( $p < 0.001$ ), perennial herbs ( $p = 0.001$ ), *Compositae* ( $p = 0.025$ ), *Chenopodiaceae* ( $p = 0.019$ ) and *Gramineae* ( $p < 0.001$ ) within the nebkha was significantly lower than in the inter-nebkha area (Fig. 5a). However, when nebkha growth was stable, the richness of these species within the nebkhas was significantly higher compared to the inter-nebkha area (Fig. 5b). Interestingly, the density of perennial herbs ( $p < 0.001$ ), *Chenopodiaceae* ( $p = 0.021$ ) and *Gramineae* ( $p = 0.033$ ) was significantly higher within the nebkhas

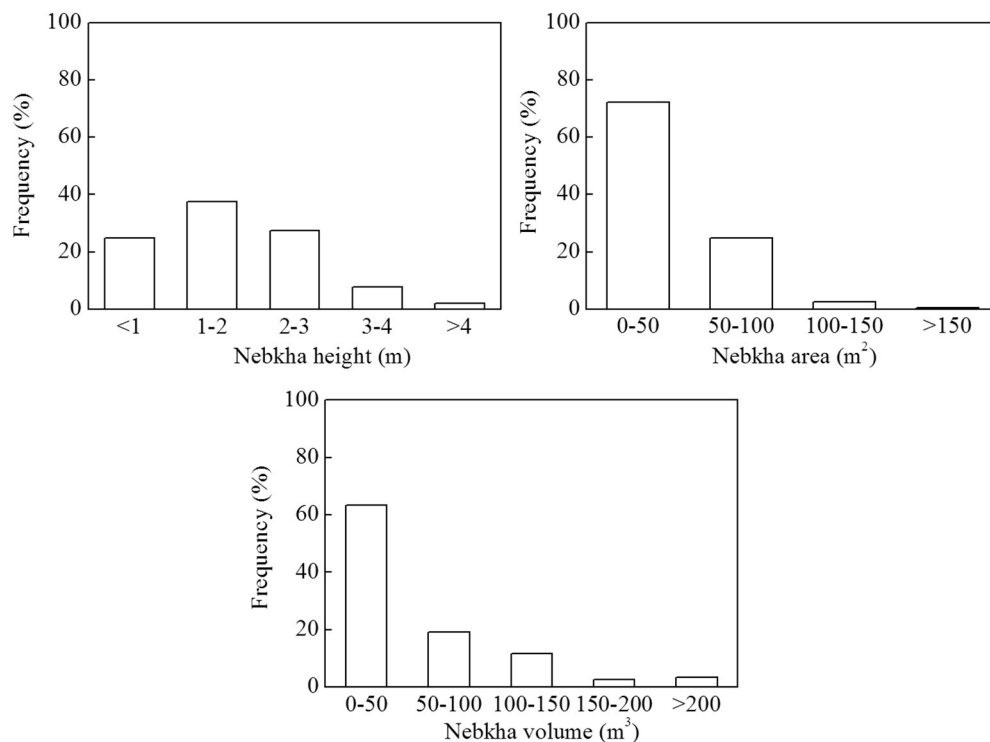


Fig. 3. Morphology parameter statistics of nebkhas.

**Table 2**

Frequency of plants found in nebkhas and inter-nebkha areas. (AH, annual herb; ABH, annual-biennial herb; PH, perennial herb; Co, Compositae; Ch, Chenopodiaceae; Gr, Gramineae.).

Location	Total	Herbaceous			Shrubs	Family			
		AH	ABH	PH		Co	Ch	Gr	Others
Nebkhas	45	21	3	18	3	7	10	13	15
Inter-nebkha areas	49	21	3	21	4	8	10	13	18

than in the inter-nebkha areas during nebkha growth as well as stabilization (Fig. 5c, d). The densities of annual herbs ( $p = 0.006$ ) and Compositae ( $p = 0.016$ ) within the nebkhas, on the other hand, were smaller than in the inter-nebkha areas during nebkha growth stabilization (Fig. 5d).

### 3.3. Relationship between species richness and size of nebkhas

Species richness and the richness of herbs, in particular, increased with the enlargement of the nebkha area when nebkhas were in growing stage following a linear relation with  $R^2$ -values of 0.69 and 0.61, respectively (Fig. 6a, c). In contrast, the density of plants decreased, following a logarithmic function ( $R^2 = 0.74$ ), with the increase of area in growth stages of nebkhas (Fig. 6e). Notably, similar correlations between the species richness, richness of herbs and the density of species within the nebkha area were found when nebkhas were in stabilizing stage ( $R^2 = 0.07$ ,  $R^2 = 0.01$ ,  $R^2 = 0.15$ ) (Fig. 6b, d, f).

## 4. Discussion

### 4.1. Characteristics of nebkhas and species composition

The size of nebkhas is highly dependent on the species associated with it (Du et al., 2010), the volume of sand in the area (Al-Dousari et al., 2008; Khalaf et al., 1995; Tengberg and Chen, 1998) and the plant density found on nebkha mounds (El-Bana et al., 2002). The chief regulatory factor that controls the shape and size of the nabkha deposits in the desert steppe is the height of the shrub it is associated with (Khalaf et al., 1995). For example, the sand trapping ability of *Gazaniais* is significantly greater per unit area and forms elongated nabkhas that are high, narrow, and conical in shape, while *Arctotheca* forms short, semi-circular nabkhas (Hesp and McLachlan, 2000). This is because the *Arctotheca populifolia* has a prostrate growth habit and is relatively spread out, while the *Gazania rigens* has a vertical, dense, multi-branching growth habit. *N. tangutorum* also has a dense, multi-branching growth habit; thus the sand trapping ability of *N. tangutorum* is greater per unit area and forms elongated nabkhas that are high. The morphological characteristics of *N. tangutorum* may

thus explain why the average size of the nebkhas studied here is much smaller than other shrub nebkhas that were reported for *Tamarix ramosissima* in the Taklamakan desert and Ejin Banner of China (Qong et al., 2002; Wang et al., 2008), but larger than the *Caragana microphylla* nebkhas in Northeast China (Wang et al., 2006; Hasi et al., 2013). All nebkhas reach their full height when they are fully developed and in a stabilized condition (Tengberg and Chen, 1998; Hasi et al., 2013). In our study, the height/width and height/length ratios were approximately 0.30 and 0.24 respectively, indicating that individual *N. tangutorum* expanded horizontally rather than vertically. That indicated that most nebkhas in this area were still at the growth stage (Hasi et al., 2013).

In our study, the majority of species found on nebkhas were herbs, and in particular annual herbs. Similarly, approximately 89% of species found on nebkhas in the coastal habitats of Kuwait are also herbs (El-Sheikh et al., 2010). Nebkhas provide good shelter for many halophyte and glycophyte herb species (Al-Dousari et al., 2008; El-Bana et al., 2002). The spatial heterogeneity of therophytes may be due to the heterogeneous moisture conditions near the soil surface. Many of these sites represent favorable microsities, where moisture seepage can occur around the host shrubs of the nebkhas (Brown and Porembski, 1997, 2000; Noy-Meir, 1973; El-Sheikh et al., 2010). Thus, the characteristics of the host plants can dictate plant diversity on nebkhas, and directly influence the community composition and richness among nebkhas (El-Bana et al., 2007). However, it seems that the order in which species associate to a specific nebkha host is not random, with few species, predominantly annuals and dwarf species, associated to the early successional nebkhas and a large subset of species, mostly perennial herbs and geophytes, recruiting in large and diverse late successional nebkhas (El-Bana et al., 2007).

### 4.2. Species richness in nebkhas and adjacent habitat

The species composition and the soil physicochemical properties of nebkhas are very different from those of the inter-nebkha areas (El-Bana et al., 2003; Isermann, 2005). We show that species richness in the inter-nebkha areas was significantly higher compared to the nebkha itself during the development phase, but significantly lower when nebkhas were fully formed. This discrepancy may be related to the fact that the fertile island effect was not observed during the early developmental stage of the nebkhas, and so, soil litter and resources may not have been efficiently accumulated under the small canopies of the young plants (Zhang et al., 2011). During the later developmental stages of nebkhas, fertile islands are present and the nebkhas are richer in organic matter, silt and clay than the inter-nebkha area (Abd El-Wahab and Al-Rashed, 2010). It is possible that the competition capacity among the host species changes throughout the different developmental stages of the nebkhas, which leads to a high variation of species richness. Nebkhas formed by different species also result in the variation in community structure, because differences in canopy size of the nebkha building plants lead to different competition capacity. For example, woody, nitrogen fixing legumes such as *Retama raetam* may enhance soil nutrient content and improve soil structure, this lead to high species richness on *R. raetam* nebkhas (El-Bana et al., 2007). The soil content and plant biodiversity of the nebkhas are preserved and increased by host shrubs, since shrubs work effectively to trap water, soil materials and propagules from other areas (El-Bana et al., 2002). Compared with the inter-dune areas, the large canopies over fully developed nebkhas also provide a suitable microenvironment for seed survival by limiting direct solar radiation and high soil temperature (Domingo et al., 2000; El-Bana et al., 2003). One advantage of nebkhas was that their building plants have the potential to preserve plant diversity in overgrazed plant communities, because they are effective in capturing and retaining water, and propagules within and from nearby areas, resources that would otherwise be lost (El-Bana et al., 2007). Thus, nebkha plays an important role in the ecological and evolutionary dynamics of many desert ecosystems, especially in land restoration of arid and semiarid environments.

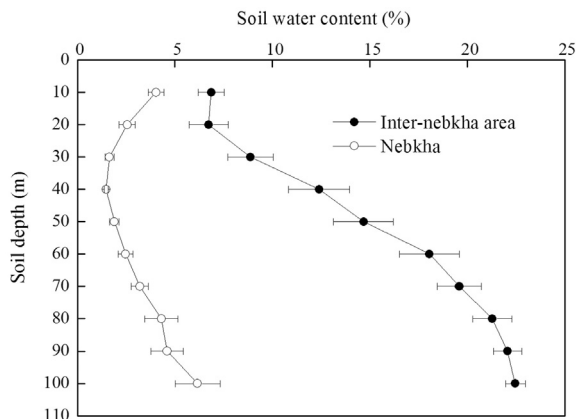
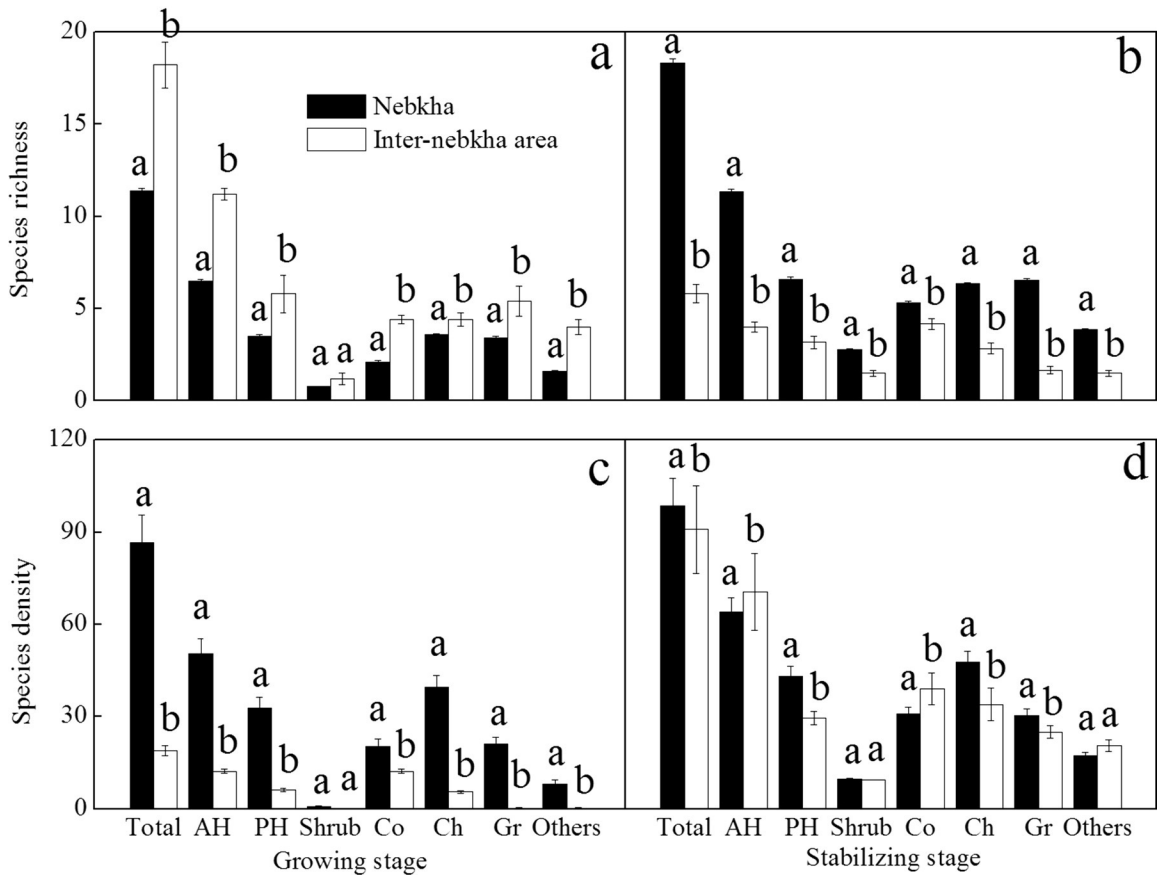
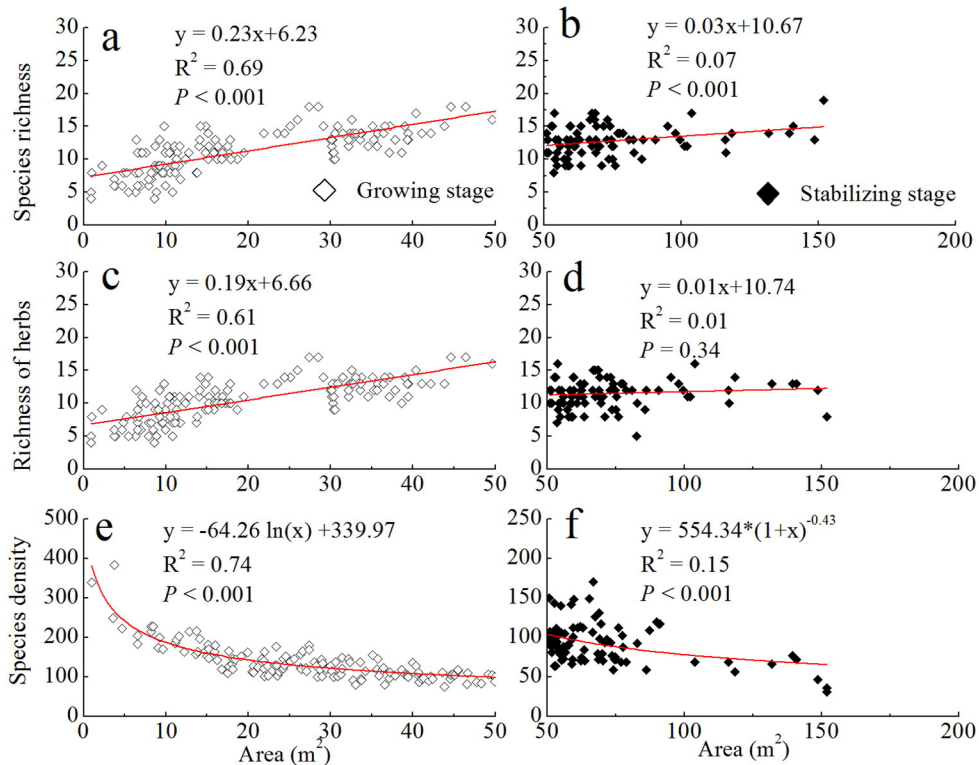


Fig. 4. Soil water content of nebkhas and inter-nebkha areas (mean  $\pm$  SE,  $n = 20$ ).



**Fig. 5.** Differences in species richness and densities on nebkhas and inter-nebkha areas in different growth stages (mean  $\pm$  SE). (AH, annual herb; PH, perennial herb; Co, Compositae; Ch, Chenopodiaceae; Gr, Gramineae.); differing letters indicate a significant difference between nebkhas and inter-nebkha area ( $p < 0.05$ ); the same letter indicates a non-significant difference ( $p > 0.05$ ).



**Fig. 6.** Relationship between species richness (a, b), richness of herbs (c, d), density of species (e, f) and area of nebkhas in different growth stages.

In arid and semiarid regions, water availability in the soil is the most critical factor that controls the productivity and reproduction of plants (Noy-Meir, 1973). In this study, we found that the level of soil moisture inside the developing nebkhas was less than in the inter-nebkha area. Since rainfall will flow away from the nebkhas and collect in the inter-nebkha area, there is a higher level of soil moisture in the inter-nebkha area. The low level of soil moisture on nebkhas may limit the establishment of herbaceous plants, and cause the presence of herbaceous plants on *Caragana tibetica* nebkhas to be very limited (Zhang et al., 2011). However, at some sites, extreme soil erosion occurred in the inter-nebkha area and caused a redistribution of fine soil particles and nutrients to the nebkhas (El-Bana et al., 2002), and a switch in species distribution. As a nebkha-building plant, the *N. tangutorum* has developed a root system where the majority of roots are found 0–40 cm below the surface (Sun and Yu, 1992; Li, 2010). Thus, this host species competes with other species for the limited water content in the nebkhas and makes it difficult for other species to invade. Brown and Porembski (1997, 2000) found that plant diversity within the nebkhas was higher when the environmental conditions were the harshest (Brown and Porembski, 1997, 2000). Therefore, under ideal environmental conditions, nebkhas appear to have little advantage for plant growth over the inter-nebkha areas.

#### 4.3. Relationship between species richness and size of nebkhas

Both environmental (total nitrogen, moisture content, organic carbon and soil temperature) and non-environmental characteristics (host canopy area, species number and nebkha area) of the nebkhas have significant influences on species distribution within nebkha patches (El-Bana et al., 2007). Conversely, the form and growth of host species may greatly influence both environmental and non-environmental features of the nebkhas (Hesp and McLachlan, 2000). For instance, the abundance and richness of the plant species *R. raetam* were dependent on the size of the nebkha (El-Bana et al., 2003). The species richness and nested distribution had a positive species–area relationship within nebkhas (El-Bana et al., 2007; El-Bana, 2009). Correspondingly, we found that species richness increased with the enlargement of the nebkha area and this pattern applied to both herbaceous plants and shrubs, conforming to the species–area curve, when nebkhas were still in growing stage. The explanation is that the greater distribution and density of plants in larger nebkhas are likely the result of an increase to the seed bank size (Brown and Porembski, 2000), and a greater distribution of soil nutrients (Hesp and McLachlan, 2000; El-Bana et al., 2002).

Herbaceous plant densities and shrub sizes, but not height, have been shown to have a positive linear relationship with the area of the nebkha (El-Bana et al., 2002). This was not evident in our study, since the plant density decreased with the enlargement of nebkha area in both developing and fully-developed stages. Plant interactions can greatly affect plant distribution and diversity (Brooker, 2006) such that the host species can affect the richness and density of other species. In some conditions, the host species acts as a nurse plant and protects their understory species, causing the species density in nebkhas to be higher than in the inter-nebkha area. At our study site, these positive interactions were likely weakened with the enlargement of the nebkha area and lead to decreases in plant density.

## 5. Conclusion

In desert steppe areas, morphological characteristics of nebkhas are important factors regulating species richness and composition within the region. The species richness within the nebkhas varied greatly from that in the inter-nebkha areas during different developmental periods. During the developmental stages, the inter-nebkha areas provided more favorable conditions for plant survival than the nebkhas; however, plant survival of annual and perennial herbs in particular, was more greatly supported in the nebkhas that had fully developed.

## Acknowledgements

We would also like to thank Dr. Angela Scott at the McMaster University for her assistance with English language and grammatical editing of the article. We also gratefully acknowledge the journal's anonymous reviewers for their valuable comments on our article. This work was financially supported by the project of National Basic Research Program of China (No. 2013CB429903).

## Appendix A

A list of all species involved in this study. AH = annual herb, ABH = annual–biennial herb, PH = perennial herb, S = shrub, SS = semi-shrub. P = psammophyte, N = nebkha, IN = inter-nebkha area.

Species	Family	Life form	Habitats		
<i>Artemisia frigida</i> Willd	Compositae	PH	N, IN		
<i>Artemisia ordosica</i> Krasch		S	N, IN		
<i>Artemisia scoparia</i> Waldst. et Kit.		ABH	N, IN		
<i>Artemisia sieversiana</i> Ehrhart ex Willd		ABH	N, IN		
<i>Echinops gmelini</i> Turcz		AH	N, IN		
<i>Heteropappus altaicus</i> (Willd.) Novopokr		PH	N, IN		
<i>Ixeridium graminifolium</i> (Ledeb.) Tzvel		PH	N, IN		
<i>Mulgedium tataricum</i> (L.) DC		PH	IN		
<i>Saussurea japonica</i> (Thunb.) DC		PH	N, IN		
<i>Saussurea laciniata</i> Ledeb		PH	N, IN		
<i>Scorzonera divaricata</i> Turcz		PH	N, IN		
<i>Agriophyllum squarrosum</i> (L.) Moq		Chenopodiaceae	AH	N, IN	
<i>Atriplex centralasiatica</i> Iljin			AH	N, IN	
<i>Bassia dasyphylla</i> (Fisch. et C. A. Mey.) Kuntze			AH	N, IN	
<i>Chenopodium acuminatum</i> Willd	AH		N, IN		
<i>Chenopodium aristatum</i> L.	AH		N, IN		
<i>Corispermum chinganicum</i> Iljin	AH		N, IN		
<i>Kochia scoparia</i> (L.) Schrad.	AH		N, IN		
<i>Salsola collina</i> Pall	AH		N, IN		
<i>Salsola passerine</i> Bunge	AH		N, IN		
<i>Suaeda salsa</i> (L.) Pall.	AH		N, IN		
<i>Agropyron cristatum</i> (L.) Gaertn	Gramineae		PH	N, IN	
<i>Chloris virgata</i> Sw.			AH	N, IN	
<i>Cleistogenes squarrosa</i> (Trin.) Keng			PH	N, IN	
<i>Eragrostis pilosa</i> (L.) Beauv			AH	N, IN	
<i>Setaria viridis</i> (L.) Beauv		AH	N, IN		
<i>Stipa capillata</i> L.		PH	N, IN		
<i>Pennisetum centrasaticum</i> Tzvel. Pl. As. Centr		PH	N, IN		
<i>Phragmites australis</i> (Cav.) Trin. ex Steud		PH	IN		
<i>Oxytropis racemosa</i> Turcz		Leguminosae	PH	N, IN	
<i>Sophora alopecuroides</i> L.			AH	N, IN	
<i>Sphaerophysa salsula</i> (Pall.) DC.			PH	N, IN	
<i>Thermopsis lanceolata</i> R. Br			PH	N, IN	
<i>Euphorbia humifusa</i> Willd. ex Schlecht.			Euphorbiaceae	AH	N, IN
<i>Euphorbia kozlovii</i> Prokh				PH	N, IN
<i>Polygonum sibiricum</i> Laxm.	Polygonaceae		PH	N, IN	
<i>Incarvillea sinensis</i> Lam	Bignoniaceae		AH/PH	N, IN	
<i>Messerschmidia sibirica</i> L.	Boraginaceae		PH	N, IN	
<i>Glaux maritime</i> L.	Primulaceae		PH	N, IN	
<i>Cynanchum chinense</i> R. Br.	Asclepiadaceae		AH	N, IN	
<i>Cynanchum hancockianum</i> (Maxim.) Al. Iljinski			PH	N, IN	
<i>Cynanchum thesioides</i> (Freyn) K. Schum.			S	IN	
<i>Hypecoum erectum</i>	Papaveraceae		AH	N, IN	
<i>Limonium aureum</i> (L.) Hill	Plumbaginaceae	AH	N, IN		
<i>Silene odoratissima</i> Bge	Caryophyllaceae	AH	N, IN		
<i>Stellaria gypsophiloides</i> Fenzl		PH	IN		
<i>Cuscuta chinensis</i> Lam.	Convolvulaceae	AH	N, IN		

## References

- Abd El-Wahab, R.H., Al-Rashed, A.R., 2010. Vegetation and soil conditions of phytogenic mounds in Subiya area Northeast of Kuwait. *Catrina* 5 (1), 87–95.
- Aguiar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trees* 14, 273–277.
- Al-Dousari, A., Ahmed, M., Al-Senafy, M., 2008. Characteristics of nebkhas in relation to dominant perennial plant species in Kuwait. *Kuwait J. Sci.* 35, 127–150.
- Armas, C., Pugnaire, F., 2005. Plant interactions govern population dynamics in a semiarid plant community. *J. Ecol.* 93, 978–989.

- Batanouny, K.H., 2001. Plants in the deserts of the Middle East. In: Cloudsley-Thompson, J.L. (Ed.), *Adaptation of Organisms to the Desert*. Springer Verlag, Heidelberg, p. 193.
- Brooker, R.B., 2006. Plant–plant interactions and environmental change. *New Phytol.* 171, 271–284.
- Brown, G., Porembski, S., 1997. The maintenance of species diversity by miniature dunes in a sand-depleted *Haloxylon salicornicum* community in Kuwait. *J. Arid Environ.* 37, 461–473.
- Brown, G., Porembski, S., 2000. Phytogenic hillocks and blow-outs as 'safe sites' for plants in an oil-contaminated area of northern Kuwait. *Environ. Conserv.* 27, 242–249.
- Cabrera-Vega, L.L., Cruz-Avero, N., Hernández-Calvento, L., Hernández-Cordero, A.I., Fernández-Cabrera, E., 2013. Morphological changes in dunes as an indicator of anthropogenic interferences in arid dune fields. *J. Coast. Res.* (65).
- Carrera, A.L., Bertiller, M.B., Sain, C.L., Mazzarino, M.J., 2003. Relationship between plant nitrogen conservation strategies and the dynamics of soil nitrogen in the arid Patagonian Monte, Argentina. *Plant Soil* 255, 595–604.
- Crawley, M.J., Herral, J.E., 2001. Scale dependence in plant biodiversity. *Science* 291, 864–868.
- Domingo, F., Villagarcía, L., Brenner, A.J., Puigdefabregas, J., 2000. Measuring and modelling the radiation balance of a heterogeneous shrubland. *Plant Cell Environ.* 23, 27–38.
- Du, J.H., Yan, P., Dong, Y.X., 2010. The progress and prospects of nebkhas in arid areas. *J. Geogr. Sci.* 20, 712–728.
- El-Bana, M.I., 2009. Factors affecting the floristic diversity and nestedness in the islets of Lake Bardawil, North Sinai, Egypt: implication s for conservation. *J. Coast. Conserv.* 13, 25–37.
- El-Bana, M.I., Li, Z.Q., Nijs, I., 2007. Role of host identity in effects of phytogenic mounds on plant assemblages and species richness on coastal arid dunes. *J. Veg. Sci.* 18, 635–644.
- El-Bana, M.I., Nijs, I., Khedr, A.H.A., 2003. The importance of phytogenic mounds (nebkhas) for restoration of arid degraded rangelands in northern Sinai. *Restor. Ecol.* 11, 317–324.
- El-Bana, M.I., Nijs, I., Kockelbergh, F., 2002. Microenvironmental and vegetational heterogeneity induced by phytogenic nebkhas in an arid coastal ecosystem. *Plant Soil* 247, 283–293.
- El-Sheikh, M.A., Abbadi, G.A., Bianco, P.M., 2010. Vegetation ecology of phytogenic hillocks (nebkhas) in coastal habitats of Jal Az-Zor National Park, Kuwait: role of patches and edaphic factors. *Flora* 205, 832–840.
- Gao, S.Q., Pan, X., Cui, Q.G., Hu, Y.K., Ye, X.H., Dong, M., 2014. Plant interactions with changes in coverage of biological soil crusts and water regime in Mu Us sandland, China. *PLoS One* 9, e87713.
- Hasi, E., Du, H.S., Sun, Y., 2013. *Caragana microphylla* nebkhas in Inner Mongolia Plateau: morphology and surface airflow. *Quat. Sci.* 33 (2), 314–324.
- He, Z.B., Zhao, W.Z., Chang, X.X., Chang, X.L., Fang, J., 2005. Scale dependence in desert plant diversity. *Biodivers. Conserv.* 15, 3055–3064.
- Hesp, P., McLachlan, A., 2000. Morphology, dynamics, ecology and fauna of *Arctotheca populifolia* and *Gazania rigens* nebkhas. *J. Arid Environ.* 44, 155–172.
- Holzappel, C., Mahall, B.E., 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. *Ecology* 80, 1747–1761.
- Isermann, M., 2005. Soil pH and species diversity in coastal dunes. *Plant Ecol.* 178, 111–120.
- Khalaf, F.I., Misak, R., Al-Dousari, A., 1995. Sedimentological and morphological characteristics of some nebkha deposits in the northern coastal plain of Kuwait, Arabia. *J. Arid Environ.* 29, 267–292.
- Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., Lavorel, S., 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond. B Biol.* 270, 775–781.
- Li, H.R., 2010. Studying on the process of *Nitraria tangutorum* nebkhas' growth between oasis and desert (Master's thesis) Gansu Agricultural University.
- Link, S.O., Waugh, W.J., Downs, J.L., Thiede, M.E., Chatters, J.C., Gee, G.W., 1994. Effects of coppice dune topography and vegetation on soil water dynamics in a cold-desert ecosystem. *J. Arid Environ.* 27, 265–278.
- Liu, S., Bai, J., Jia, Z., Jia, L., Zhou, H., Lu, L., 2010. Estimation of evapotranspiration in the Mu Us Sandland of China. *Hydrol. Earth Syst. Sci.* 14, 573–584.
- Liu, Z.M., Li, X.L., Yan, Q.L., Wu, J.G., 2007. Species richness and vegetation pattern in interdune lowlands of an active dune field in Inner Mongolia, China. *Biol. Conserv.* 140, 29–39.
- Magurran, A., 2004. *Measuring Biological Diversity*. Blackwell, Malden.
- Nickling, W.G., Wolfe, S.A., 1994. The morphology and origin of nebkhas, region of Mopti, Mali, West Africa. *J. Arid Environ.* 28, 13–30.
- Nishimori, H., Tanaka, H., 2001. A simple model for the formation of vegetation dunes. *Earth Surf. Process. Landf.* 26, 1143–1150.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annu. Rev. Ecol. Syst.* 4, 25–51.
- Okin, G.S., 2013. Linked Aeolian–Vegetation Systems. In: Shroder, J.F. (Ed.) *Treatise on Geomorphology* vol. 11. Academic Press, San Diego, pp. 428–439.
- Parsons, A.J., Wainwright, J., Schlesinger, W.H., Schlesinger, W.H., Abrahams, A.D., 2003. The role of overland flow in sediment and nitrogen budgets of mesquite dunefields, southern New Mexico. *J. Arid Environ.* 53, 61–71.
- Pool, M.R., Pool, S.K., Parvaneh, I., Dehghani, Z., Rostamian, M., 2013. Nebkhas of *Salvadora persica* and their effect on the growth and survival of *Prosopis cineraria*, *Tamarix aphylla*, and *Capparis decidua* trees and shrubs. *Flora* 208, 502–507.
- Qong, M., Takamura, H., Hudaberd, M., 2002. Formation and internal structure of *Tamarix* cones in the Taklimakan Desert. *J. Arid Environ.* 50, 81–97.
- Rango, A., Chopping, M., Ritchie, J., Havstad, K., Kustas, W., Schmutge, T., 2000. Morphological characteristics of shrub coppice dunes in desert grasslands of southern New Mexico derived from scanning LIDAR. *Remote Sens. Environ.* 74, 26–44.
- le Roux, P.C., Shaw, J.D., Chown, S.L., 2013. Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New Phytol.* 200, 241–250.
- Schenk, H.J., Mahall, B.E., 2002. Positive and negative plant interactions contribute to a north-south-patterned association between two desert shrub species. *Oecologia* 132, 402–410.
- Schlesinger, W.H., Raikes, J.A., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77, 364–374.
- Shen, Y., 2008. Study on the dynamic characteristics of desertification grassland vegetation and the effects of fencing improvement in Yanchi of Ningxia, (Master's thesis). Beijing Forestry University.
- Stock, W.D., Dlamini, T.S., Cowling, R.M., 1999. Plant induced fertile islands as possible indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa. *Plant Ecol.* 142, 161–167.
- Su, Y.Z., Yang, R., Zhang, Z.H., Du, M.W., 2012. Distribution and characteristics of *Nitraria sphaerocarpa* nebkhas in a Gobi habitat outside an oasis in Hexi Corridor region, China. *Sci. Cold Arid Reg.* 4, 0288–0295.
- Su, Y.Z., Zhao, W.Z., Su, P.X., Zhang, Z.H., Wang, T., 2006. Ecological effects of desertification control and desertified land reclamation in oasis-desert ecotone in an arid region: a case study in Hexi Corridor, Northwest China. *Ecol. Eng.* 29, 117–124.
- Sun, X., Yu, Z., 1992. A study on root system of *Nitraria tangutorum*. *J. Desert Res.* 12, 50–54 (in Chinese with English abstract).
- Team for Comprehensive Surveying in Inner Mongolia and Ningxia Autonomous Regions (TCSIMNAR), 1985a. *Vegetation in Inner Mongolia*. Science Press, Beijing (in Chinese).
- Tengberg, A., 1995. Nebkha dunes as indicators of wind erosion and land degradation in the Sahel zone of Burkina Faso. *J. Arid Environ.* 30, 265–282.
- Tengberg, A., Chen, D.L., 1998. A comparative analysis of nebkhas in central Tunisia and northern Burkina Faso. *Geomorphology* 22, 181–192.
- Titus, J.H., Nowak, R.S., Smith, S.D., 2002. Soil resource heterogeneity in the Mojave Desert. *J. Arid Environ.* 52, 269–292.
- Vasek, F.C., Lund, L.J., 1980. Soil characteristics associated with a primary plant succession on a Mojave Desert dry lake. *Ecology* 61, 1013–1018.
- Wang, X., Wang, T., Dong, Z., Liu, X., Qian, G., 2006. Nebkha development and its significance to wind erosion and land degradation in semi-arid northern China. *J. Arid Environ.* 65, 129–141.
- Wang, X.M., Xiao, H.L., Li, J.C., Qiang, M.R., Su, Z.Z., 2008. Nebkha development and its relationship to environmental change in the Alaxa Plateau, China. *Environ. Geol.* 56, 359–365.
- Wood, M.K., Blackburn, W.H., Eckert, R.E., Peterson, F.F., 1978. Interrelations of the physical properties of coppice dune and vesicular dune interspace soils with grass seedling emergence. *J. Range Manag.* 31, 189–192.
- Yan, Q.L., Liu, Z.M., Zhu, J.J., Luo, Y.M., Wang, H.M., Jiang, D.M., 2005. Structure, pattern and mechanisms of formation of seed banks in sand dune systems in northeastern Inner Mongolia, China. *Plant Soil* 277, 175–184.
- Zhang, P.J., Yang, J., Zhao, L.Q., Bao, S., Song, B.W., 2011. Effect of *Caragana tibetica* nebkhas on sand entrapment and fertile islands in steppe-desert ecotones on the Inner Mongolia plateau, China. *Plant Soil* 347, 79–90.
- Zhou, H., Zhao, W.Z., Luo, W.C., Liu, B., 2015. Species diversity and vegetation distribution in nebkhas of *Nitraria tangutorum* in the Desert Steppes of China. *Ecol. Res.* 30 (4), 735–744.