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Original Research

Changes in Morphology of *Nitraria tangutorum* Nebkhas at different Successional Stages in the Oasis-Desert Ecotone, Northwest China

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Abstract

Nebkhas play a tremendous role in maintaining the ecological functions of deserts and in slowing land desertification processes. Numerous nebkhas are distributed in the northwestern edge of the Ulan Buh desert, *Nitraria tangutorum* nebkhas are the most typical dunes in this area. However, our knowledge of the effect of those factors on the succession of nebkhas, including their succession in different sandy land types, is limited. The goal of this study was to reveal their factors influencing the morphological characteristics of *N. tangutorum* nebkhas in different sandy land types (shifting sandy land, semi-fixed sandy land, and fixed sandy land) in the Ulan Buh desert. Our results showed the densities of *N. tangutorum* nebkhas were 34, 51, and 77 dunes per ha in the shifting, semi-fixed, and fixed sandy lands, respectively. The density of *N. tangutorum* nebkhas gradually increased and *N. tangutorum* nebkhas started to degenerate with the increasing fixation of sandy land. The successional stage had significant effects on all the morphological characteristics, and sandy land types had significant effects on the length (L), height (H), volume (V), horizontal scale (D) and ratio of width to height (H/W). Almost all of the morphological parameters of *N. tangutorum* nebkhas were correlated at different successional stages, indicating a strong interrelationship among the morphological parameters of nebkhas. The successional stages of *N. tangutorum* nebkhas had significant effects on the density of branch (M), height (h), coverage (C), deadwood rate (DR), and length of new branches (LB) of the *N. tangutorum* shrub. The M, h, C, and LB first increased and then decreased, and DR increased with the succession of *N. tangutorum* nebkhas. These results indicated that we should focus on nebkhas succession to ensure the ecological stability of oases in a dessert.

Keywords: *N. tangutorum*, nebkhas, morphological characteristics, successional stage, sand fixing capacity, sandy land types

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Introduction

Deserts cover an area of about 1.3 million km^2 in northwestern China and are expanding into adjacent ecosystems due to climate change and human activities [1-2]. The nebkha is a constructive and dominant species endemic to arid and semi-arid regions. The nebkha controls the local landscape in northwest China due to its unique ability to fix sand, and plays an important ecological role in preventing or slowing down the movement of sand particles [3]. Therefore, the succession of nebkhas is a key ecological factor in the maintenance of regional ecological security in arid environmental systems.

Nebkha, formed by the accumulation sand near shrubs in the landscape that reduce the sand carrying capacity of the of sand-saturated wind when encountering an obstacle, is one of the main types of sanddune landscape [4-6]. Their appearance is ubiquitous in arid and semi-arid desert environments with hot and desert climates [7]. In China, nebkha is mainly distributed in the agro-pastoral ecotone, desert steppe, and desert margins [8]. Their formation is determined by several factors such as climate change [9], vegetation degradation, anthropogenic activities, and changes in local hydrogeological conditions [10-13]. Nebkhas have attracted little attention concerning their succession and vegetation features. Most studies are focused on community composition and richness [8, 14-15], soil nutrients [8,16-17], ecological adaptation [18-19] and developmental processes [20-22]. However, there is much more that needs to be studied about nebkhas. The formation and disintegration of nebkhas are closely related to the positive and negative processes of land desertification, and the invasion of the species forming nebkhas is synonymous with massive nutrient loss and increased soil erosion in the desertification process [23]. It can be seen that the successional stage of nebkhas can indirectly reflect the process of land desertification [4]. Currently, there is not enough evidence to establish the relationship between the appearance of nebkhas and vegetation types and terrain. The quantitative description of the formation and succession of nebkhas is still pending.

The formation of nebkhas is closely related to the environmental conditions [18, 24]. Undoubtedly, the morphological characteristics of nebkhas can reflect the characteristics of wind and sand environment and land desertification at the spatio-temporal scale [25]. On a large scale, the characteristics of deposition and morphology in nebkhas formed can appear different due to conditions such as wind conditions, physical sources, vegetation types, and surface conditions in different regions [8]. Among them, plant type and sand conditions strongly influence the morphological characteristics of the developing nebkhas [22]. The morphological parameters of nebkhas are not uniform under different habitat conditions, but exhibit characteristics that are adapted to the local aeolian sand environment [26]. With the same observation area, distinct subsurface conditions exhibit different influences on the starting wind speed, leap height, and energy attenuation of sand grains, making the wind-sand flux and structure show obvious spatial differences along the wind direction, and the abundance of sand supply affects the spatial scale of nebkhas. Therefore, nebkhas are localized and complex. On a small scale, the size and shape of nebkhas will depend on factors such as plant growth habit, plant density, and structural form [21, 26-27]. It is by plants changing the structure of near-surface wind and sand flow in three ways that nebkhas are formed: plants providing the ground coverage, slowing down the wind and blocking the flow of sand [27]. It is believed that surface vegetation coverage is the most effective measure to control wind erosion in arid and semi-arid regions, especially in the desert-oasis transition zone of northern China.

Few researchers have examined the effects of sandy land type, successional stage, and vegetation features on the morphological characteristics of *N. tangutorum* nebkhas in the oasis-desert ecotone. The research on morphological characteristics of *N. tangutorum* nebkhas on different sandy land types in an oasis-desert ecotone can effectively provide a theoretical basis and support for the protection and rehabilitation of oasis-desert ecotones in hyperarid regions. In this research, we (1) evaluated the relationships between nebkhas density and sandy land types, (2) quantitatively analyze the effect of succession on the morphological characteristics of *N. tangutorum* nebkha, and (3) determined whether different successional nebkhas have different influences in terms of morphology and vegetation characteristics.

Materials and Methods

Study Area

The study was carried out in the oasis-desert ecotone in Jilantai Township, Inner Mongolia, China (39°38′-39°49′N, 105°35′-105°46′E). The average elevation is 1020-1030 m. The climate of the Jilantai desert oasis ecotone is arid, with a temperate continental monsoon climate. Precipitation amounts to 102.2 mm yr^{1} but is highly variable, and most of which occurs between July and September (1965-2020). The potential annual evaporation is 29.4 times higher than the precipitation with 3006 mm. The long-term mean annual temperature is approximately 8.60ºC, and the annual sunshine is 3316 h. The prevailing wind direction is northwesterly. The mean annual wind speed is 3.54 m/s, and occasionally up to 15 m/s. The total mean annual typical day with strong winds is 34 d. The region has typically fixed dunes without any human interference. This landscape consists of nebkhas of different sizes covered by aeolian sandy soils. The vegetation is dominated by the shrub species *N. tangutorum*. The common psammophytic vegetation includes *Agriophyllum squarrosum, Salsola collina, Artemisia desertorum, Achnatherum splendens, Phragmites australlis* and *Sophora alopecuroides*.

Experimental Design and Methods

We defined four succession stages of nebkhas based on our morphometric measurements, vegetation status and combined with the experience of previous studies [28-30]. Successional stages of *N. tangutorum* nebkhas were classified based mainly on the mortality rate of branches of *N. tangutorum*, and *N. tangutorum* nebkhas were divided into rudimental stage (RUD), developing stage (DEV), stabilizing stage (STA), and degrading stage (DEG).

Fieldwork was carried out in August 2019. We selected three sample plots with different sandy land types, representing shifting sandy land, semi-fixed sandy land, and fixed sandy land (Fig. 1). In the field investigation, we selected 3 plots (100 m×100 m) in each sandy land type. The distance between plots was no more than 20 m. The wind conditions, precipitation, and other natural factors of *N. tangutorum* nebkhas are similar, and the basic situation of the sample plot is shown in Table 1. In each plot, the morphology of all *N. tangutorum* nebkhas was measured, including length (L), width (W), height (H), windward slope length (Y), leeward slope length (B), and horizontal scale (D). In total, the study examined 507 nebkhas. The sand axis along the main wind direction is defined as length (L), and the sand axis perpendicular to the main wind direction is defined as W. The H of nebkha was calculated as the mean heights in four directions. The length of the distance from the bottom of windward slope to the top of nebkha is Y. The same method was used to determine the B. The D was calculated using the formula $[(L+W)/2]$.

The base area (A_1) and volume (V_1) of shield-shaped nebkhas were calculated as follows:

$$A_1 = \frac{1}{2}WL \tag{1}$$

$$V_1 = \frac{1}{6}WLH \tag{2}$$

The base area (A_2) and volume (V_2) of cone-shaped nebkhas were calculated as follows:

$$A_2 = \frac{1}{4}\pi WL \tag{3}$$

$$V_2 = \frac{1}{12}\pi HWL \tag{4}$$

The base area (A_3) and volume (V_3) of hemi-ellipsoid nebkhas were calculated as follows:

Fig.1. Sample plots of the different sandy land types in the oasis-desert ecotone of Jilantai Township.

Table 1. Basic characteristics of different sandy land types.

Sandy land types	Latitude and longitude	Altitude/m	Vegetation coverage/%	Soil type	Associated species
Shifting sandy land	105°43′12″E-39°48′48″N	999	3.12±1.05c	Windy sandy soil, hard calcareous layer	*Agriophyllum squarrosum*, *Salsola collina*
Semi-fixed sandy land	105°43′17″E-39°48′40″N	983	25.66±6.79b	Windy sandy soil, hard calcareous layer	*Calligonum mongolicum*, *Haloxylon ammodendron*, *Artemisia desertorum*, *Agriophyllum squarrosum*
Fixed sandy land	105°43′28″E-39°48′21″N	972	65.35±12.44a	Windy sandy soil	*Achnatherum splendens*, *Phragmites australlis*, *Sophora alopecuroides*

Note: Values are means±SD. Different lowercase letters in the same column represent significant differences of *N. tangutorum* indices among different successional stages (P<0.05).

$$A_3 = \frac{1}{4}\pi WL \tag{5}$$

$$V_3 = \frac{1}{6}\pi HWL \tag{6}$$

Twenty *N. tangutorum* nebkhas in the successional stage were randomly selected for measuring their shrub characteristics, shrub parameters including the density of branch (*M*), height (*h*), coverage (*C*), deadwood rate (*DR*), and length of new branch (*LB*) of *N. tangutorum* shrub. Five small quadrats (1.0 m×1.0 m) were set at the top, midslope and bottom of windward, and midslope and bottom of windward of nebkha, respectively. The *C* was estimated by calculating the vertical projection area ratio for vegetation in each small quadrat. The *M* was determined by counting the number of individuals in each small quadrat. The *h* is the natural height of *N. tangutorum*. The *DR* was estimated by the sampling method as the ratio of the projected area of dead branches in the quadrat to the quadrat area. The *LB* of the current year was measured in each sample square. New branch length was calculated by measuring the natural length of newborn branches in the current year in each small quadrat. The mean values of 5 small quadrats were taken as the mean value of nebkha.

Statistical Analysis

The coefficient of variation (C_v) is used to express the variation of nebkhas' morphometric parameter data in the different successional stages. Statistics were performed using the SPSS 21.0 software package (SPSS, Inc., Chicago, IL, USA). Statistical significance was determined with one-way ANOVA analysis. We used two-way ANOVA to test the effects of sandy land type (SL) and successional stage (SS) on morphological characteristics. Figures and regression analysis were drawn with Origin 9.0 (Origin Lab, Northampton, MA, USA).

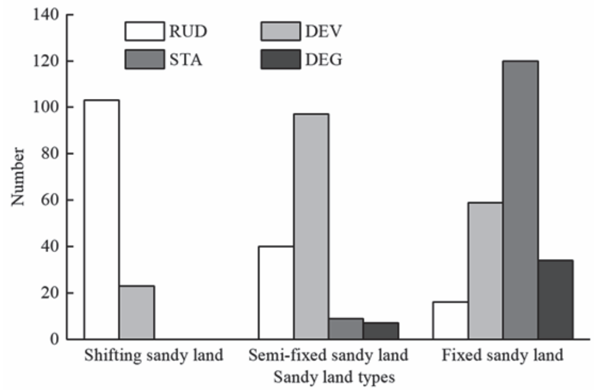

Fig. 2. The number of different successional stages of *N. tangutorum* nebkhas in different sandy land types. RUD:rudimental stage; DEV:developing stage; STA:stabilizing stage; DEG:degrading stage.

Results

Characteristics of *N. tangutorum* Nebkhas in Different Sandy Land Types

The density of *N. tangutorum* nebkhas was 34, 51 and 77/hm^2 in shifting sandy land, semi-fixed sandy land and fixed sandy land, respectively. In shifting sandy land, *N. tangutorum* nebkhas in RUD dominated 81.76%, and the rest are all *N. tangutorum* nebkhas in DEV. No *N. tangutorum* nebkhas in STA and DEG in shifting sandy land. In semi-fixed sandy land, *N. tangutorum* nebkhas in RUD, DEV, STA, and DEG

Table 2. Characteristics of *N. tangutorum* nebkhas in different successional stages.

Successional stage	Height/m	Nebkha characteristics	*N. tangutorum* Characteristics	Form
RUD	<1.0	The nebkha is short, with a large head and small tail, irregularly shaped, with a long tail of wind shadow, and a relatively gentle slope.	Most of *N. tangutorum* branches are newborn and have a white appearance.	Shield shape
DEV	1.0~5.0	The nebkha is large with steep slopes.	*N. tangutorum* grows luxuriantly, with white skin. *Phragmites australlis* and other plants are occasionally seen on nebkhas	Cone-shape
STA	1.0~2.0	The nebkha is large with steep slopes.	*N. tangutorum* branches are denser, gray, or black in appearance, with a lot of *Phragmites australlis* and other plants settling on the surface.	Semi-ellipse
DEG	0.5~1.5	The nebkha is short, and the slope is uneven and low.	The *N. tangutorum* is in weak growth condition with a black appearance and a large number of exposed roots.	Semi-oval

Note: Values are means±SD. Different lowercase letters in the same column represents significant differences of *N. tangutorum* indices in different successional stages ($P<0.05$). RUD:rudimental stage; DEV:developing stage; STA:stabilizing stage; DEG:degrading stage

Table 3. Results of ANOVA for the effect of sandy land type and successional stage on morphological parameters of *N. tangutorum* nebkhas.

Factors	Effect	*L*	*W*	*H*	*Y*	*B*	*A*	*V*	*D*	*H*/*L*	*H*/*W*
Sandy land types (ST)	*F*	6.75	0.55	6.68	6.75	0.55	4.42	8.24	4.42	2.46	3.25
	P	0.001***	0.577	0.001***	0.001***	0.577	0.013	<0.001***	<0.05*	0.086	<0.05*
Successional stage (SS)	*F*	159.28	90.24	286.33	159.28	90.24	176.02	89.39	176.02	146.62	107.48
	P	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***
ST×SS	*F*	15.26	13.01	19.30	15.26	13.01	19.78	16.77	19.78	0.53	0.30
	P	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***	0.72	0.88

Note: F-values (*F*) and associated probabilities (*P*) are shown, with significant experimental effects indicated by asterisks (*P<0.05; **P<0.01; ***P<0.001). RUD:rudimental stage; DEV:developing stage; STA:stabilizing stage; DEG:degrading stage

were 40, 97, 9, and 7, respectively. *N. tangutorum* nebkhas in DEV accounted for the largest proportion of all successional stages (63.40%), *N. tangutorum* nebkhas in RUD accounted for 26.14%, and it started to appear *N. tangutorum* nebkhas in STA and DEG. In fixed sandy land, abundant *N. tangutorum* nebkhas occurred at STA and DEG. Among them, *N. tangutorum* nebkhas in DEV and STA accounted for 25.76% and 52.40%, respectively.

A two-way ANOVA analysis demonstrated that sandy land types had significant effects on *L*, *H*, *V*, *D*, and *H*/*W*, and successional stage had significant effects on all the morphological characteristics. There were significant interactive effects of sandy land type and the

Table 4. The morphological characteristics of different successional stages of nebkhas.

Successional stage	Index	*L*/m	*W*/m	*H*/m	*Y*/m	*B*/m	*A*/m^2	*V*/m^3	*D*/m	*H*/*L*	*H*/*W*
RUD	Mean±SD	5.20± 1.27d	4.32± 1.19d	0.67± 0.15d	6.93± 1.7d	3.03± 0.83d	7.49± 1.81d	9.18± 6.64d	4.76± 1.15d	0.13± 0.01c	0.16± 0.02c
	Maximum	8.9	7.41	1.1	11.87	5.19	12.84	37.95	8.16	0.18	0.23
	Minimum	3.01	2.08	0.38	4.01	1.46	4.03	1.27	2.56	0.10	0.12
	C_v/%	24.47	27.42	21.9	24.47	27.42	24.12	72.35	24.12	8.78	12.29
DEV	Mean±SD	9.95± 2.99a	6.99± 2.02a	1.68± 0.47a	13.26± 3.99a	4.89± 1.41a	13.34± 3.49a	73.54± 63.95a	8.47± 2.22a	0.17± 0.02b	0.24± 0.04a
	Maximum	8.86	4.34	1.29	11.81	3.04	10.39	26.07	6.60	0.15	0.30
	Minimum	5.45	3.70	1.05	7.27	2.59	7.73	12.90	4.91	0.13	0.18
	Cv/%	30.09	28.91	28.21	30.09	28.91	26.18	86.96	26.18	10.99	17.18
STA	Mean±SD	8.28± 2.53b	6.21± 0.63b	1.50± 0.29b	11.04± 3.37b	4.35± 0.44b	11.41± 2.49b	42.71± 24.49b	7.24± 1.58b	0.18± 0.02a	0.24± 0.02a
	Maximum	10.06	6.66	1.71	13.42	4.66	13.16	60.03	8.36	0.20	0.26
	Minimum	6.49	5.76	1.29	8.65	4.03	9.65	25.4	6.13	0.17	0.22
	Cv/%	30.54	10.18	19.47	30.54	10.18	21.81	57.32	21.81	11.41	9.39
DEG	Mean±SD	7.1± 0.79c	5.65± 1.84c	1.24± 0.12c	9.47± 1.06c	3.96± 1.29c	10.04± 0.82c	25.83± 7.97c	6.38± 0.52c	0.18± 0.04b	0.23± 0.05b
	Maximum	7.66	6.96	1.32	10.21	4.87	10.62	31.46	6.75	0.20	0.26
	Minimum	6.54	4.35	1.15	8.72	3.05	9.46	20.19	6.01	0.15	0.19
	Cv/%	11.17	32.53	9.40	11.17	32.53	8.20	30.84	8.20	20.46	23.48

Note: *L*, *W*, *H*, *Y*, *B*, *C*, *A*, *V*, *D*, *H*/*W* and *H*/*L* represent the length, width, height, windward slope length, leeward slope length, circumference, area, volume, horizontal scale, ratio of height and width and the ratio of height and length of *N. tangutorum* nebkhas. RUD:rudimental stage; DEV:developing stage; STA:stabilizing stage; DEG:degrading stage successional stage on *L*, *W*, *H*, *Y*, *B*, *A*, *V*, *D*, *H/L* and *H/W* (Table 3).

The morphological parameters of the *N. tangutorum* nebkhas in the oasis-desert ecotone varied significantly along the succession from the RUD to the DEG. Except for H/L and H/W, all parameters increased from RUD to DEV and then decreased in DEG ($P<0.05$). Furthermore, H/L and H/W, which were indicators of the degree of expansion, also increased significantly with the successional stage ($P<0.05$), meaning that the horizontal expansion speed of *N. tangutorum* nebkhas was greater than the vertical expansion speed in the oasis-desert ecotone. Except for V, the C_v of *N. tangutorum* nebkhas' morphological parameters in different successional stages were smaller. This indicated that morphological parameters of nebkhas at each successional stage did not differ significantly.

Almost all of the morphological parameters of *N. tangutorum* nebkhas have a good correlation at different successional stages, which indicated a strong interrelationship among the morphological parameters of nebkhas (Table 5). The height was significantly and positively correlated to nebkha length, width, horizontal scale, area, and volume, respectively. Significant correlations were also observed between length and width, between windward slope length, and leeward slope length, as well as between area and volume, respectively.

Table 5. Correlation coefficients between morphological parameters of *N. tangutorum* nebkhas.

Successional stage	Form parameters	*L*	*W*	*H*	*Y*	*B*	*A*	*V*	*D*	*H/L*	*H/W*
RUD (n = 159)	*L*	1.000									
	W	0.747 **	1.000								
	H	0.937 **	0.928 **	1.000							
	Y	1.000 **	0.747 **	0.937 **	1.000						
	B	0.747 **	1.000 **	0.928 **	0.747 **	1.000					
	A	0.939 **	0.930 **	0.998 **	0.939 **	0.930 **	1.000				
	V	0.900 **	0.897 **	0.956 **	0.900 **	0.897 **	0.962 **	1.000			
	D	0.939 **	0.930 **	0.998 **	0.939 **	0.930 **	1.000 **	0.962 **	1.000		
	H/L	-0.439 **	0.242 **	-0.109	-0.439 **	0.242 **	-0.118	-0.112	-0.118	1.000	
	H/W	-0.012	-0.643 **	-0.333 **	-0.012	-0.643 **	-0.338 **	-0.321 **	-0.338 **	-0.821 **	1.000
DEV (n = 179)	*L*	1.000									
	W	0.548 **	1.000								
	H	0.917 **	0.819 **	1.000							
	Y	1.000 **	0.548 **	0.917 **	1.000						
	B	0.548 **	1.000 **	0.819 **	0.548 **	1.000					
	A	0.924 **	0.825 **	0.992 **	0.924 **	0.825 **	1.000				
	V	0.835 **	0.825 **	0.972 **	0.835 **	0.825 **	0.940 **	1.000			
	D	0.924 **	0.825 **	0.992 **	0.924 **	0.825 **	1.000 **	0.940 **	1.000		
	H/L	-0.399 **	0.472 **	-0.018	-0.399 **	0.472 **	-0.054	0.103	-0.054	1.000	
	H/W	0.563 **	-0.343 **	0.239 **	0.563 **	-0.343 **	0.224 **	0.171 *	0.224 **	-0.836 **	1.000

Table 5. Continued.

STA (n = 129)	*L*	1.000									
	W	0.214 *	1.000								
	H	0.841 **	0.702 **	1.000							
	Y	1.000 **	0.214 *	0.841 **	1.000						
	B	0.214 *	1.000 **	0.702 **	0.214 *	1.000					
	A	0.853 **	0.692 **	0.996 **	0.853 **	0.692 **	1.000				
	V	0.788 **	0.752 **	0.972 **	0.788 **	0.752 **	0.984 **	1.000			
	D	0.853 **	0.692 **	0.996 **	0.853 **	0.692 **	1.000 **	0.984 **	1.000		
	H/*L*	-0.657 **	0.553 **	-0.165	-0.657 **	0.553 **	-0.190 *	-0.121	-0.190 *	1.000	
	H/*W*	0.586 **	-0.612 **	0.095	0.586 **	-0.612 **	0.106	-0.013	0.106	-0.894 **	1.000
DEG (n = 41)	*L*	1.000									
	W	0.428 **	1.000								
	H	0.811 **	0.876 **	1.000							
	Y	1.000 **	0.428 **	0.811 **	1.000						
	B	0.428 **	1.000 **	0.876 **	0.428 **	1.000					
	A	0.811 **	0.876 **	1.000 **	0.811 **	0.876 **	1.000				
	V	0.769 **	0.897 **	0.992 **	0.769 **	0.897 **	0.992 **	1.000			
	D	0.811 **	0.876 **	1.000 **	0.811 **	0.876 **	1.000 **	0.992 **	1.000		
	H/*L*	-0.035	0.883 **	0.553 **	-0.035	0.883 **	0.553 **	0.591 **	0.553 **	1.000	
	H/*W*	0.454 **	-0.585 **	-0.136	0.454 **	-0.585 **	-0.136	-0.189	-0.136	-0.876 **	1.000

Note: (*) Correlation significant at the $P<0.05$ level; (**) Correlation is significant at the $P<0.01$ level. *L*, *W*, *H*, *Y*, *B*, *C*, *A*, *V*, *D*, *H*/*W* and *H*/*L* represent the length, width, height, windward slope length, leeward slope length, circumference, area, volume, horizontal scale, ratio of height and width and ratio of height and length of *N. tangutorun* nebkhas. RUD:rudimental stage; DEV:developing stage; STA:stabilizing stage; DEG:degrading stage.

Relationship between Morphological Parameters of *N. tangutorum* nebkhas

To reflect the development of *N. tangutorum* nebkhas at different successional stages, we performed regression analyses of the morphological parameters. As shown in Fig. 3a), the regression relationship between nebkha *L* and *W* fitted to quadratic and parabolic functions in STA and maintained a linear and increasing trend in RUD, DEV, and DEG, respectively.

The regression relationship between *D* and *H* of nebkhas, between *L* and *H* of nebkhas, between *W* and *H* of nebkhas, and *A* and *H* of nebkhas illustrated significant linearly increasing trends in all successional stages, respectively (Fig. 3b,c,e,f). These results revealed that the nebkha horizontal scale, length, width and area increased with the height of *N. tangutorum* nebkhas at all successional stages, respectively.

The regression relationship between *B* and *Y* of nebkhas fitted to quadratic and parabolic functions in DVE and STA, and maintained a linear and increasing

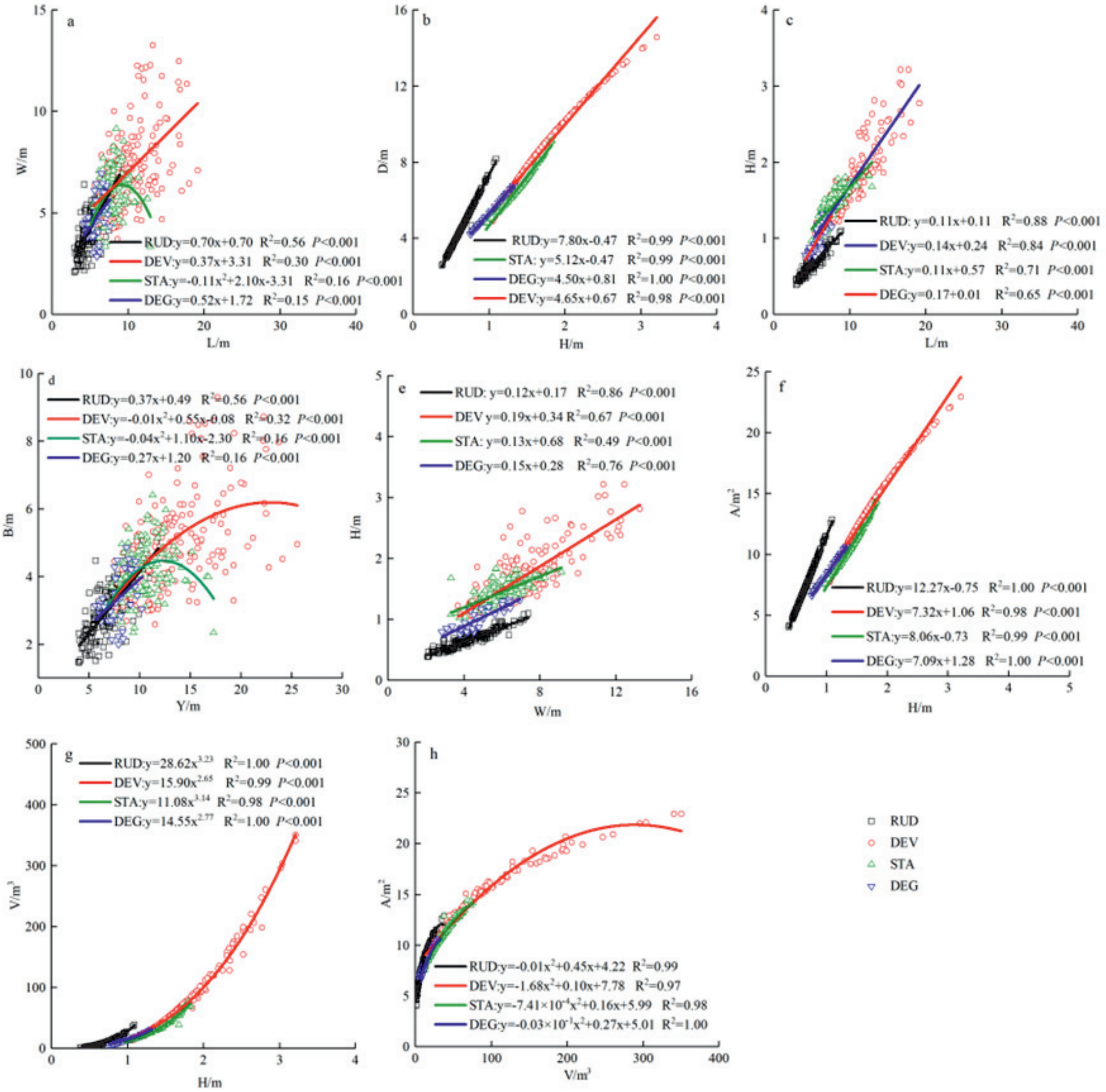

Fig. 3. Regression relationships between morphological parameters of *N. tangutorum* nebkhas in different successional stages. RUD:rudimental stage; DEV:developing stage; STA:stabilizing stage; DEG:degrading stage.

trend in RUD and DEG, respectively (Fig. 3d). However, the regression relationship between *H* and *V* of nebkhas fitted to power functions in all successional stages, which were found to best fit on nebkhas size from the study area (Fig. 3g).

The regression relationship between *A* and *V* of nebkhas fitted to the second-order polynomial functions in all successional stages (Fig. 3h). In both RUD, STA, and DEG, the fitted trend curves go up over the entire time domain. Yet, in DEV, the fitted trend curve rises at the beginning. Since then, it becomes slightly flat and then shows a slightly decreasing trend.

Vegetation Growth of *N. tangutorum* in Different Sandy Land Types

As shown in Table 6, the developmental stage of *N. tangutorum* nebkhas had significant effects on *M*, *h*, *C*, *DR*, and *LB*. The *M*, *h*, *C*, and *LB* showed firstly increased and then decreased, and *DR* showed an increasing trend with the succession of *N. tangutorum* nebkhas. For *M* and *C*, the *M* and *C* of *N. tangutorum* shrubs at DEV were both significantly higher than other successional stages ($P<0.05$). For *h*, the h of *N. tangutorum* shrubs at STA was significantly higher than RUD and DEV ($P<0.05$). For *DR*, the *DR* of *N. tangutorum* shrubs at DEG was significantly higher than other successional stages ($P<0.05$). For *LB*, the *LB* of *N. tangutorum* shrubs at DEV was significantly higher than at STA and DEG.

Discussion

Characteristics of *N. tangutorum* nebkhas in Different Sandy Land Types

In this study, the *H*/*L* and *H*/*W* of *N. tangutorum* nebkhas ranged from 0.14 to 0.17 and 0.17 to 0.24 at different successional stages, indicating that the

Table 6. Vegetation characteristics of N. tangutorum nebkhas in different successional stages.

Developmental stage	*M*/(number/m^2)	*h*/cm	*C*/%	*DR*/%	*LB*/cm
RUD	10.37±3.21b	22.49±2.77c	16.22±4.36c	3.55±0.58d	11.12±3.27ab
DEV	22.12±10.55a	34.86±7.17bc	45.77±10.66a	9.56±2.25c	15.69±5.55a
STA	13.47±5.69b	45.42±2.88a	35.44±8.88b	25.69±7.88b	7.41±1.13c
DEG	8.11±2.58c	37.85±6.67ab	14.33±3.28c	40.36±11.25a	5.14±1.15cd

Note: Values are means±SD. Different lowercase in the same column represents significant differences of *N. tangutorum* indices in different successional stages (P<0.05). RUD:rudimental stage; DEV:developing stage; STA:stabilizing stage; DEG:degrading stage.

horizontal growth rate of *N. tangutorum* nebkhas is much greater than the vertical growth rate, which is a growth strategy of *N. tangutorum* nebkhas due to self-protection. Our results were in accordance with both Toranjzar et al. [31] and Yang et al. [32]. The morphological parameters of nebkhas are important indexes for desertification monitoring, and the morphological characteristics of nebkhas are driven by shrub, sand sources, and climatic factors [33]. In this study, the morphology is closely related to sandy land types and succession (Table 3). The density of *N. tangutorum* nebkhas increased gradually with sand fixation (Fig. 2). The key reason was vegetation coverage, that is to say, the vegetation coverage of shrubs gradually increases as the sand become fixed, thereby increasing its interception of sand material and promoting the formation of nebkhas [34-35]. In addition, in this study, the size of the *N. tangutorum* nebkhas gradually increased as the sand became fixed. One reason for this phenomenon is the distance from sand source, *N. tangutorum* nebkhas adjacent to the sand source are subject to strong wind erosion and are less likely to form larger *N. tangutorum* nebkhas. The *N. tangutorum* nebkhas adjacent to the sand source is also greatly damaged by wind and sand, thus limiting the growth condition of *N. tangutorum* and eventually affecting the accumulation of *N. tangutorum* nebkhas [36]. Another important reason is that the development time of *N. tangutorum* nebkhas remote from the sand source is earlier, and some *N. tangutorum* nebkhas have developed to STA, when all morphological parameters of *N. tangutorum* nebkhas have reached the maximum. Therefore, large *N. tangutorum* nebkhas generally formed in the fixed sandy land.

Relationship between Morphological Parameters of *N. tangutorum* Nebkhas

This study found that there was a good correlation among morphological parameters of *N. tangutorum* nebkhas at different successional stages, indicating that the succession of *N. tangutorum* nebkhas was synergistic in different sandy land types [37]. In this study, the regression relationship between nebkha length and width fitted to quadratic and parabolic functions in STA (Fig. 3a). Our result was often at odds with those reported by Yan et al. [37] who showed that the regression relationship between nebkha length and width maintained a linear and increasing trend. It can be inferred that length and width of *N. tangutorum* nebkhas may simultaneously increase in RUD and DEV, and tended to be STA when the long axis reached -b/2a, or wind erosion and activation start from both sides of the windward side of *N. tangutorum* nebkhas, and the activated substances deposit on the leeward side of *N. tangutorum* nebkhas, resulting in the increase of length [21], thereby accelerating *N. tangutorum* nebkhas into DEG. In this study, the height of *N. tangutorum* nebkhas at different successional stages is a linear function of horizontal scale, and this result was often at odds with both Tengberg and Chen [38] and Tengberg [5]. Who showed that the height and horizontal scale of nebkhas follow quadratic functions. This suggests that there was a strong correlation between height and horizontal scale, regardless of the successional stage of *N. tangutorum* nebkhas. Then, we conclude that it is irrelevant to determine the successional stage of nebkhas by the relationship between height and horizontal scale in isolation.

The Morphology and Development of Shrub Determines the Succession of Nebkhas

In arid and semi-arid regions, *N. tangutorum* nebkha is one of the most abundant and widely distributed nebkhas. Nevertheless, variations in climate and environment have motivated *N. tangutorum* nebkhas to new characteristics to cope with the complexity of the ecology [14]. In this study, according to field observations, the overall morphology of *N. tangutorum* nebkhas appears on approximate shield shape, cone-shape, or semi-ellipse. This is essentially the same finding as described by Li et al. [39], as mention above. This is likely because nebkha landscapes are dynamic at different successional stages, as the growth status of nebkhas often changes to adapt to the external environment. Several studies have suggested that morphological variation was associated with both successional stage of nebkha and ecological characteristics of *N. tangutorum* [5-6, 39]. In this study, the mean height of the nebkhas formed *N. tangutorum* nebkha was between 0.38 m and 1.50 m, which was much larger than those reported for *Retama raetam* nebkhas in the Lake Bardawi [6], but smaller than *Tamarix* nabkhas in Hotan River Basin, Xinjiang [39]. This has been attributed largely to shrub characteristics. The height of nebkhas is determined by certain plant attributes [22]. Due to *N. tangutorun* has a prostrate growth habit, sand sources in the study area is abundant and *N. tangutorum* forms numerous sprouting branches after being buried. Sand burial stimulated photosynthesis in buried *N. tangutorum*, and transferred biomass allocation from belowground to aboveground parts, and promoted the growth state of *N. tangutorum* in a good direction [40-41]. As a result, the shrub size and the sediment interception increase [18, 35].

Zhu [42] and Sun et al. [43] found that the growth status of shrubs affected the formation and succession of nebkhas, only when the vegetation height exceeds 10~15 cm could effectively intercept fine sand material. The larger the density of plant branches is, the smaller the plant permeability is, and the stronger the intercepting ability of sand grains is. When the vegetation coverage exceeds 15%, surface wind erosion can be effectively controlled [44]. In this study, we found that the density, height, coverage, deadwood rate and length of new branch of *N. tangutorum* shrubs were directly related to the size and succession of nebkha [20]. Our data showed that *N. tangutorum* shrubs have a certain ability to fix sand, and especially at DEV, which has the strongest wind-proof and sand-fixing ability. Yet, the vegetation coverage ranged from 14.3 to 43.8% at different successional stages, thus leading to the *N. tangutorum* nebkhas being in a mounded state at other successional stages, whereas the *N. tangutorum* nebkhas being in a wind erosion state at DEG, and the size of *N. tangutorum* nebkhas decreases and finally disappears. Several previous studies have found that large nebkhas can conserve and increase soil moisture and nutrient content which stimulated the growth and activity of soil microorganisms, and promoted plant growth [14, 20, 45]. In this study, the length of new branch showed an increase, then decreasing trend with *N. tangutorum* nebkhas succession, indicating that in RUD and EDV, wind-deposited sand accumulated among roots, growing shoots, and shoots of *N. tangutorum*, thus driving the development of *N. tangutorum* nebkhas. However, when *N. tangutorum* nebkhas developed to DEV and DEG, an excessive amount of sand mass piles up within nebkhas, leading to insufficient air within the nebkhas and consequently to the necrosis of *N. tangutorum*, which led to the destruction and degradation of *N. tangutorum* nebkhas. Conversely, the deadwood rate of *N. tangutorum* gradually increased with successional stage, sparse near-ground branch coverage makes sand accumulation unfavorable. Shrub characteristics were similar to those of succession of nebkha, confirming previous observations.

Conclusions

Through the field investigation of 507 *N. tangutorum* nebkhas in three sandy land types (shifting sandy land, semi-fixed sandy land, and fixed sandy land), we found that the successional processes of *N. tangutorum* nebkhas were classified. Large morphological variations existed between successional stages, implying that the sand fixation capacity of *N. tangutorum* nebkhas changed in different successional stages. The converging effects of shrubs on *N. tangutorum* nebkhas formation and sand fixation capacity increased with increasing nebkhas size. We conclude that the morphology and size of *N. tangutorum* nebkhas were governed by successional stage, sandy land type, and vegetation growth. However, much remains to be learned about the relationship between morphological parameters and shrub types. The results indicated that *N. tangutorum* nebkhas in the study area is in the middle and early stages of succession due to the abundant supply of sand, and characterized by high density and small size in the landscape. If the expansion of desert into the oasis is to be stopped, more emphasis on the management of the nebkhas in the area will be necessary, especially *N. tangutorum* nebkhas, which are in the degrading stage.

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Conflict of Interest

The authors declare no conflict of interest.

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