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Assessment of the effects of phytogenic nebkhas on soil nutrient accumulation and soil microbiological property improvement in semi-arid sandy land

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ABSTRACT

Phytogenic nebkhas formed by shrubs, widely distributed in arid and semiarid ecosystems, commonly results in the patchiness of vegetation and strongly affect the spatial distribution of soil resources. In this study, we investigated the soil nutrient contents (organic matter, total N and P, and available N, P, and K), enzymatic activities (polyphenol oxidase, phosphomonoesterase, dehydrogenase, urease, and protease), and microbial community level physiological profiles for carbon source utilization in varying soil depths in different microsites within nabkhas, under the crown, and outside nabkhas of *Caragana microphylla*, *Atraphaxis manshurica*, and *Salix gordejevii* nebkhas in the western Horqin Sandy Land in Northeast China. Our main objectives were to determine whether "islands of fertility" developed both within and under the crown of the three nabkha types, to test whether the effects of islands of fertility differ among nebkha types, and to study the spatial heterogeneities of soil microbiological properties. Soil nutrients decreased with soil depth and with the distances from the center of each nebkha. The three nebkha types all created spatially heterogeneous patterns of soil nutrient within and around the nebkhas. Island of fertility effect varied among the nebkha types. *C. microphylla* nebkha had the highest enrichment ratios in soil organic matter and available N and P, whereas *A. manshurica* had the highest ratios in total N and P, and *S. gordejevii* had the highest ratio in available K. Phytogenic nebkhas also increased soil enzymatic activities and functional diversity for carbon source utilization of soil microflora. Enzyme activities among the microsites varied with enzyme type and shrub species. Phytogenic nebkhas can be considered major sources of soil nutrient and heterogeneity in microbiological property in the semi-arid ecosystem. Thus, more attentions to the management of phytogenic nebkhas should be considered in ecological restoration practices in semi-arid regions.

1. Introduction

Desertification or land degradation in arid or semi-arid areas is attracting attention as it is a global problem affecting 25% of the total land area on earth (Kassas, 1995; Reynolds et al., 2007). Common in desertified areas are phytogenic mounds (nebkhas), usually named "fertile islands", "resource islands", or "islands of fertility" (Schlesinger et al., 1996; Carrera et al., 2003; Li et al., 2010), which prevent soil erosion and nutrient loss. Shrub nebkhas supply high concentrations of soil nutrients, thereby affecting species diversity, distributions of plant and soil microbe, and productivity of plant communities (Schlesinger and Pilmanis, 1998). Thus, shrub nebkhas are important in the ecological restoration of desertified lands. Shrub nebkhas in arid or semi-arid regions are often formed from wind and water erosions, which lead to uneven microtopography and the patchy distribution of soil. Along with this is the accumulation of plant litter underneath the shrubs more than in the surrounding bare lands, thereby resulting in uneven distribution of soil nutrients. Spatial heterogeneity of soil properties and nutrient contents result from heterogeneous plant distribution, e.g., shrub nebkhas in arid or semi-arid land, which creates "islands" where high rate nutrient uptake and high rate of plant litter deposition in the soil occur (Rietkerk et al., 2002). Furthermore, improved environmental conditions underneath the plant crown, such as moderate temperature, higher water-holding capacity, and lower wind velocity, accelerate residue decomposition and increase

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soil nutrient contents (Aguiar and Sala, 1999; Rossi and Villagra, 2003). Studies have investigated the effect of plant-induced fertile islands on spatial variability of soil nutrients (Augustine and Frank, 2001; El-Bana et al., 2002; Li et al., 2008; Liu et al., 2011; Peng et al., 2013; Wei et al., 2013). However, fertile islands especially in sandland ecosystem, has not been sufficiently explored. How soil nutrients and microbiological properties change with soil depth within nebkhas is not yet known. Furthermore, little is known on the differences among fertile islands induced by different shrubs. Soil microbes participate in the development of "fertile islands" because they contribute to litter decomposition, nutrient cycling, enzymatic production, and aggregate stability, which affect the physical and chemical attributes of soil (Nogueira et al., 2006; Pengthamkeerati et al., 2011; Preem et al., 2012; Vasconcellos et al., 2013), However, studies on the soil enzymatic activities and microbial community level physiological profiles in nebkhas are still scarce. Horqin Sandy Land (42°41′–45°15′N, 118°35′ to 123°30′E) is a severely degraded sandy grassland in the northeast of China, where desertified land accounts for 57.8% of the total area in this region (Zhao et al., 2004). Currently, Horqin Sandy Land is one of the most severely desertified areas in China. Historically, many lakes existed in the area, and the landscape was characterized by an extended forest steppe (Zhao et al., 2004). However, with the increase in populations of domestic animals and local residents since the 1950s, the ecological landscape dramatically changed as a result of overgrazing, excessive land use, and depleted vegetation due to wood gathering for fuel. Overuse and inappropriate management of natural resources resulted in desertified grasslands. At present, the landscape is mainly characterized by an alternation of moving, semi-moving, and stabilized sand dunes. During such ecosystem conversion, shrubs, such as *Caragana mirophylla* Lam., *Atraphaxis manshurica* Kitag., and *Salix gordejevii* Chang et Skv., gradually encroached into the former grassland. The density and cover of these shrubs gradually increased, and finally many phytogenic mounds (nebkhas) formed resulting from the continuous wind erosion and aeolian accumulation. This phenomenon explains the development of the well-known "islands of fertility". In this study, we investigated three typical nebkhas in the Horqin Sandy Land, i.e., *C. mirophylla*, *A. manshurica*, and *S. gordejevii*, to determine whether "islands of fertility" has developed both within and underneath them and to test whether the islands of fertility effects differ among the three nebkha types. In addition, we also studied spatial heterogeneities of soil enzymatic activities and soil microbial metabolic function of nebkhas.

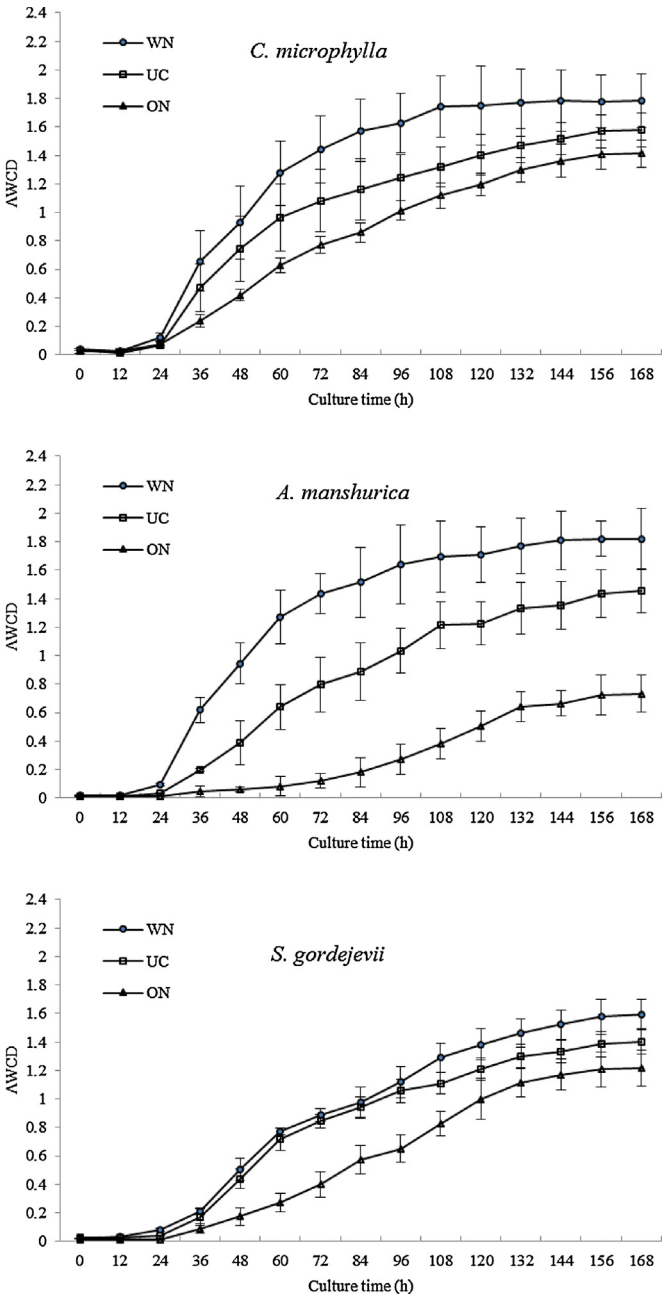

Fig. 1. Variation in average well color development (AWCD) over time in Biolog Ecoplate.
WN: within nebkha; UC: Under crown; ON: Outside nebkha. Data were generated by four replicates.

2. Materials and methods

2.1. Study location and site description

This study was conducted in Wulanaodu Region (43°02′N, 119°39′E, 480 a.s.l.), western Horqin Sandy Land of Northeast China. Wulanaodu Region is located in the temperate zone and has a semi-arid climate. According to Wulanaodu Weather Station, the annual average temperature in the area is 6.3 °C, with a frost-free period that lasts for 130 days. The annual average precipitation is 340.5 mm, 70%–80% of which is received from May to September; and the annual average pan evaporation is around 2500 mm. The annual average wind velocity is 4.4 m s^{-1}, and windy seasons occur from March to May during spring and winter, with frequent occurrence of gales (wind speeds >20 m s^{-1}). The landscape is a mosaic of moving and semi-moving sand dunes with interdune bottomland. Surface sand deposits are 20–120 m thick (Zhang et al., 2004). The soils are classified as cambic arenosols, which are susceptible to wind erosion (FAO, 2006). Strong wind erosion and sand burial on sandlands often occur from March to May. The original vegetation in the Horqin area was elm sparse woodland steppe composed of a considerable number of perennial plants, e.g., *Aneurolepidium chinense* Kitag, *Cleistogenes chinensis* Keng, *Lespedeza davurica* Schindl., *Agropyron cristatum* Gaertn., and *Stipa grandis* P. Smirn., with sparsely scattered *Ulmus pumila* L. However, most of the original vegetation was destroyed over several decades because of prolonged inappropriate use of grassland, e.g., overgrazing, excessive land use, and heavy plant harvesting (Cao et al., 2008). These activities are the major factors that cause grassland desertification and shrub encroachment. At present, the sandy land vegetation is generally dominated by some shrubs and semi-shrubs (e.g., *Caragana microphylla*, *A. manshurica*, *S. gordejevii*, and *A. halodendron*), associated with some herbaceous plants (e.g., *Pennisetum flaecidum*,

Table 1
Morphological traits of the three nebkha types (values are means ± S.D.).

Trait	Nebkha type		
	Caragana microphylla	*Atrphaxis manashurica*	*Salix gordejevii*
Location	43°00′13″ N 119°38′19″ E	43°02′27″N 119°38′24″E	43° 00′19″N 119°38′56″E
Density (clumps/100 m^2)	9	7	8
Vegetation coverage (%)	55	60	50
Mean height (cm)	85.5 ± 15.5	71.5 ± 16.7	164.1 ± 22.7
Crown diameter (cm × cm)	250 × 300	180 × 210	320 × 270
Shoot number (N)	130.6 ± 30.3	105.8 ± 20.7	187.3 ± 40.8
Single branch weight (g)	96.8 ± 20.2	87.6 ± 18.4	156.4 ± 38.5

Table 2
Soil nutrient contents in different spatial positions of three nabkha types.

Index	Depth(cm)	*Caragana microphylla*				*Atrphaxis manashurica*				*Salix gordejevii*			
		WN	UC	ON	*P*	WN	UC	ON	*P*	WN	UC	ON	*P*
pH	0 ~ 10	6.341a	6.582a	6.607a	0.201	7.581a	7.476a	7.135a	0.053	7.215a	7.041a	7.108a	0.108
	10 ~ 20	6.335a	6.241a	6.532a	0.598	7.284a	7.301a	7.224a	0.599	7.021a	6.985a	6.781a	0.090
	20 ~ 30	6.474a	6.352a	6.571a	0.658	7.227a	7.288a	7.144a	0.283	6.862a	6.882a	6.691a	0.149
	average	6.383a	6.392a	6.570a	0.775	7.364a	7.355a	7.168a	0.356	7.033a	6.969a	6.860a	0.114
Organic matter (%)	0 ~ 10	0.662a	0.343b	0.137c	0.037	1.294a	0.747b	0.322c	0.024	0.394a	0.296a	0.197a	0.246
	10 ~ 20	0.464a	0.202b	0.078c	0.014	0.307a	0.203a	0.261a	0.591	0.183a	0.145a	0.054a	0.160
	20 ~ 30	0.142a	0.164a	0.068a	0.311	0.244a	0.203a	0.221a	0.973	0.133a	0.086a	0.035a	0.343
	average	0.423a	0.236b	0.094c	0.004	0.615a	0.384a	0.268a	0.106	0.237a	0.176a	0.095a	0.119
Total P (%)	0 ~ 10	0.037a	0.035a	0.028a	0.755	0.071a	0.051b	0.038b	0.044	0.045a	0.034b	0.028b	0.008
	10 ~ 20	0.031a	0.024a	0.025a	0.867	0.035a	0.032a	0.027a	0.094	0.034a	0.023b	0.026b	0.005
	20 ~ 30	0.023a	0.021a	0.02a	0.888	0.026a	0.03a	0.024a	0.342	0.031a	0.019b	0.023b	0.015
	average	0.030a	0.027a	0.024a	0.595	0.044a	0.038b	0.030b	0.045	0.037a	0.025b	0.026b	0.001
Available P(mg kg^{-1})	0 ~ 10	11.63a	8.045a	3.627b	0.035	15.37a	9.458a	8.427a	0.063	13.76a	10.89a	10.37a	0.381
	10 ~ 20	6.096a	4.224a	2.895a	0.147	14.54a	3.429a	8.019a	0.510	7.848a	7.494a	5.227b	0.049
	20–30	2.334a	1.601a	2.185a	0.334	4.436a	3.906a	2.105a	0.127	7.415a	5.168a	2.688b	0.044
	average	6.687a	4.623a	2.902a	0.001	11.45a	5.598a	6.184a	0.154	9.673a	7.852b	6.093b	0.013
Total N (%)	0 ~ 10	0.045a	0.026b	0.025b	0.048	0.097a	0.051b	0.044b	0.025	0.026a	0.027a	0.018a	0.105
	10 ~ 20	0.027a	0.017a	0.018a	0.087	0.034a	0.024a	0.026a	0.365	0.024a	0.024a	0.015a	0.065
	20 ~ 30	0.022a	0.014a	0.02a	0.556	0.031a	0.016a	0.017a	0.056	0.024a	0.016a	0.013a	0.165
	average	0.031a	0.019b	0.021b	0.017	0.054a	0.030a	0.029a	0.045	0.025a	0.022a	0.015a	0.111
Avaiable N(mg kg^{-1})	0 ~ 10	6.881a	3.322b	1.578c	0.014	4.205a	1.817b	1.925b	0.001	2.745a	1.985b	1.407b	0.011
	10 ~ 20	2.975a	2.103a	1.174b	0.006	2.514a	1.284b	1.224b	0.009	1.696a	1.523a	0.823b	0.002
	20 ~ 30	2.623a	1.921b	1.173b	0.001	2.047a	1.223b	1.117b	<0.001	1.468a	1.286a	0.761b	0.004
	average	4.160a	2.449b	1.308b	<0.001	2.922a	1.441b	1.420b	<0.001	1.970a	1.598a	0.997b	0.001
Avaiable K(mg kg^{-1})	0 ~ 10	219.6a	172.1b	154.3b	0.044	225.9a	184.3a	146.7a	0.193	151.7a	140.3a	95.22b	0.042
	10 ~ 20	155.3a	139.7a	129.5a	0.699	185.8a	133.5a	110.6a	0.269	108.9a	101.0a	63.33b	0.009
	20 ~ 30	104.0a	134.2a	112.5a	0.206	132.3a	1.09.8a	75.48a	0.605	109.7a	58.96b	48.55b	0.001
	average	159.6a	148.7a	132.1a	0.491	181.3a	158.9a	110.9a	0.096	123.4a	100.1a	69.03b	0.001

Means in row followed by the different letter are significantly different ($P \leqq 0.05$). WN: within nabkha; UC: under crown; ON: outside nabkha.

Aristida adscensionis, *Salsola collina*, *Digitaria ciliaris*, *Agriophyllum squarrosum*, and *Calamagrostis chinesis*).

2.2. Experimental design and soil sampling

Fieldwork was conducted in September 2013 to investigate the morphometric characteristics of *C. microphylla*, *A. manshurica*, and *S. gordejevii* nebkhas in Wulanaodu Region. The density, vegetation coverage, mean height, crown diameter, and shoot count of each shrub nebkha were recorded (Table 1). We selected four sites (four replicates) for each shrub nebkha type for sampling. Each site measured 30 m × 30 m, and each site was 200 m away from the other sites. Four nebkhas of each site were randomly selected for soil sampling. To minimize the potential interactions between nebkhas, we constrained the distance to the nearest nebkha to greater than 5 m. In each nebkha, three microsites (within nebkha: WN; under crown: UC, and outside nabkha: ON) were chosen as sampling plots. Soil samples were obtained from WN, from the edge of the shrub crown, and 50 cm away the crown in four directions at the depths of 0–10, 10–20, and 20–30 cm, respectively. Sample obtained at the depth of 0–10 cm deep was collected using a shovel, whereas those obtained at 10–30 cm deep were collected using a 5 cm soil auger. Soil samples with same microsite and soil depth in each site were mixed as a pooled sample. A total of 108 soil samples (3 nabkha types × 3 microsites × 3 soil depths × 4 replicates) were collected. All samples were sieved using a 2 mm screen. Roots and other debris were discarded. Half of each sample was kept field moist in a cooler at 4 °C, and the other half was air-dried and stored at room temperature.

2.3. Soil chemical property and enzymatic activity

Soil pH was measured in a soil–water suspension (1:1 ratio). A portion of the air-dried and sieved samples was ground and passed through a 0.25 mm screen for soil organic carbon (SOC), total N, and available N analyses. SOC was measured using the $K_2Cr_2O_7$–H_2SO_4 oxidation method of Nelson and Sommers (1982). Total nitrogen was determined by the semi-micro-Kjedahl digestion method, and

Table 3
Three-way ANOVA of soil nutrient contents and enzymatic activities in different species, different spatial positions, and different soil depths.

Index	Species		Microsite		Soil depth	
	F	*P*	*F*	*P*	*F*	*P*
pH	145.428	<0.001	0.792	0.458	7.432	0.001
Organic matter	20.696	<0.001	23.036	<0.001	40.633	<0.001
Total N	25.820	<0.001	20.422	<0.001	27.358	<0.001
Available N	25.026	<0.001	63.572	<0.001	42.275	<0.001
Total P	8.194	0.001	8.027	0.001	18.093	<0.001
Available P	3.781	0.039	8.388	0.001	13.751	<0.001
Available K	1.782	0.178	16.373	<0.001	29.234	<0.001
Polyphenol oxidase	55.572	<0.001	18.983	<0.001	13.838	<0.001
Phosphomonoesterase	6.506	0.003	25.750	<0.001	60.459	<0.001
Dehydrogenase	31.690	<0.001	10.786	<0.001	22.263	<0.001
Urease	2.358	0.104	7.278	0.002	19.211	<0.001
Protease	1.782	0.178	16.374	<0.001	29.235	<0.001

available N was determined by alkali diffusion method described in Institute of Soil Science, Chinese Academy of Sciences (ISSCAS (1985)). Soil total P and available P were determined by the Olsen and Dean method, and the available K was measured by atomic absorption spectroscopy (ISSCAS, 1985).

Polyphenol oxidase activity was measured using the method described by Perucci et al. (2000) and was expressed as millimoles of catechol oxidized kg^{-1} soil h^{-1} (on dry weight basis). Alkaline phosphomonoesterase activity was determined as described by Sardans and Peñuelas (2005) and was expressed as mg *p*-nitrophenol per kilogram dry matter and incubation time. Dehydrogenase activity was determined by the reduction of triphenyltetrazolium chloride to triphenyl formazone (TPF). The dehydrogenase was measured following a modified method of the ISSCAS (1985) and expressed as the mg of the TPF released kg^{-1} soil h^{-1}. Soil urease activity was measured using urea as the substrate, and the released ammonium was assayed colorimetrically at 460 nm (Kandeler and Gerber 1988). Protease activity was determined using the method of Ladd and Butler (1972) with some modifications. Approximately, 2 g of the soil sample was incubated at 50 °C for 2 h in 5 mL of a buffered casein solution (pH 8.1) and 5 mL of TRIS buffer (50 mM, pH 8.1). The released aromatic amino acids were extracted using trichloroacetic acid (0.92 M) and were measured colorimetrically using Folin–Ciocalteu reagent. The activity was expressed as mg Tyr (tyrosine equivalents) kg^{-1} soil h^{-1}.

2.4. Microbial community level physiological profiles

Biolog Ecoplate™ (Hayward, California, USA) was used to analyze the substrate (carbon sources) utilization patterns of bacterial communities of the different soil samples. The Ecoplate contains 3 replicate wells for 31 carbon substrates (Choi and Dobbs, 1999). In this study, community level physiological profiles (CLPPs) of 0–10 cm samples were determined. However, 10–20 and 20–30 cm samples were not analyzed. After the soil samples were incubated at 25 °C for 24 h, bacterial suspensions from soil samples were prepared as follows: 5 g of fresh soil was placed into 50 mL of sterile NaCl solution (0.85%) and was shaken for 30 min at 200 rpm for homogenization. Serial dilutions were prepared up to a dilution factor of 10^{-3}. A 20 mL aliquot of each dilution was shaken for 10 min. Then, 150 μL of aliquot was added to the wells of the Biolog Ecoplate. Finally, the plates were incubated at 25 °C in the dark. Absorbance data at 590 nm in each well were recorded at regular 24 h intervals by a microplate reader (Biotech μQuant). The bacterial metabolism activity is often described in terms of average well color development (AWCD), which can be expressed as $AWCD = \Sigma[(C - R)]/31$ (Huang et al., 2012), where *C* is the optical density of the reaction well and *R* is the optical density of the control well.

2.5. Data analysis

All data were analyzed by three-way analysis of variance (ANOVA) using species, microsite, and soil depth as variables. ANOVA and multiple comparisons were used to determine the differences among the microsites. Pearson correlation coefficients were used to evaluate the relationships among the variables. All statistical analyses were performed using the SPSS (11.5) software package. A difference at $P < 0.05$ level was considered statistically significant.

3. Results

3.1. Fertile island effect

Results of the soil nutrient determination are presented in Table 2. Three-way ANOVA revealed that soil organic matter, total N and P, and available N and P varied significantly among species, among microsites, and with soil depth (Table 3). Available K varied significantly among microsites and with soil depth, whereas no significant difference was found among the species. Soil pH also varied with soil depth and among species. Soil nutrients all decreased with increase in depth and distance from the center of nebkhas. These findings suggested that nebkha type, microsite, and soil depth all induce spatial variability of soil nutrients in the sandy land. Meanwhile, one-way ANOVA with microsite as variable indicated that the nutrient entrapment ability of soil in nebkha varied among species. In 0–10 cm depth, significant differences in nutrients were found among microsites (WN, UC, and ON) with the following exceptions: total P in *C. microphylla* site; available P and K in *A. manshurica* site; and organic matter, available P, and total N in *S. gordejevii* site. The enrichment ratios (WN/ON) of soil organic matter in *C. microphylla*, *A. manshurica*, and *S. gordejevii* sites were 4.83, 4.02, and 2.00, respectively. In addition, respective enrichment ratios were computed at 1.32, 1.87, and 1.61 in soil total P; 3.21, 1.82, and 1.33 in available P; 1.80, 2.20, and 1.44 in total N; 4.36, 2.18, and 1.95 in available N; and 1.42, 1.54, and 1.59 in available K. Trends in enrichment ratios of average nutrients in 0–30 cm depth were similar to those in the 0–10 cm depth, although the values all decreased. Overall, the three nebkha types created spatially heterogeneous patterns of soil nutrients and induced accumulation of soil nutrient within and around the nebkhas, i.e., forming "islands of fertility". In addition, fertile island effect is different among the nebkhas, i.e., *C. microphylla* nebkha had the highest enrichment ratios in soil organic matter and available N and P, whereas enrichment ratios in total N and P in *A. manshurica* nebkha and available K in *S. gordejevii* nebkha were highest among the three nebkhas.

Table 4
Soil enzyme activities in different spatial positions of three nabkha types.

Index	depth(cm)	*Caragana microphylla*				*Atrphaxis manashurica*				*Salix gordejevii*			
		WN	UC	ON	*P*	WN	UC	ON	*P*	WN	UC	ON	*P*
PRA	0～10	189.9a	162.6a	155.3a	0.718	303.6a	181.1b	130.8b	0.032	243.4a	208.4a	143.3a	0.193
	10～20	132.1a	122.8a	108.0a	0.699	280.6a	122.2b	72.32b	0.090	158.6a	149.7a	97.24a	0.268
	20～30	95.27a	76.03a	71.98a	0.206	159.9a	53.35b	33.58b	0.001	75.79a	125.2a	81.91a	0.605
	average	139.1a	120.5a	111.8a	0.355	248.0a	118.9b	78.91b	0.011	159.3a	161.1a	107.5a	0.333
PHA	0～10	106.4a	87.18b	27.15c	0.044	158.6a	151.0a	91.20b	0.029	91.55a	65.93b	21.86c	0.001
	10～20	48.35a	32.55a	15.02b	0.041	55.66a	20.55b	16.09b	0.048	38.60a	27.54a	16.63a	0.100
	20～30	35.20a	25.59a	12.14b	0.022	32.55a	29.45a	15.12b	0.047	30.96a	16.44b	11.40b	0.003
	average	63.31a	48.44a	18.10b	0.030	82.27a	66.99a	40.80b	0.035	53.70a	36.64b	16.63c	0.002
UA	0～10	2.22a	1.14b	1.05b	0.021	2.20a	2.48a	1.71a	0.260	2.53a	1.76a	1.28a	0.536
	10～20	1.24a	0.77b	0.69b	0.034	1.16a	0.92a	0.80a	0.058	1.36a	1.05a	0.72a	0.572
	20～30	1.07a	0.65b	0.62b	0.044	1.72a	0.66a	0.73a	0.105	1.20a	0.75a	0.67a	0.491
	average	1.51a	0.85b	0.79b	0.046	1.69a	1.35a	1.08a	0.201	1.70a	1.19a	0.89a	0.552
POA	0～10	0.60a	0.35a	0.36a	0.148	0.87a	0.87a	0.86a	0.990	0.68a	0.51a	0.50a	0.056
	10～20	0.49a	0.37a	0.47a	0.353	0.63a	0.61a	0.62a	0.176	0.58a	0.49a	0.48a	0.112
	20–30	0.47a	0.46a	0.45a	0.234	0.59a	0.49a	0.45a	0.202	0.53a	0.48a	0.48a	0.201
	average	0.52a	0.39a	0.43a	0.292	0.70a	0.66a	0.64a	0.302	0.60a	0.49a	0.49a	0.322
DHA	0～10	0.27a	0.24a	0.16a	0.311	0.18a	0.10a	0.10a	0.102	0.29a	0.23a	0.17a	0.084
	10～20	0.17a	0.14a	0.13a	0.628	0.11a	0.09a	0.09a	0.068	0.20a	0.19a	0.16a	0.276
	20～30	0.15a	0.13a	0.12a	0.283	0.10a	0.09a	0.08a	0.066	0.15a	0.14a	0.14a	0.523
	average	0.20a	0.17a	0.14a	0.333	0.13a	0.09a	0.09a	0.099	0.21a	0.19a	0.16a	0.358

Means in row followed by the different letter are significantly different ($P \leqq 0.05$). WN: within nabkha; UC: under crown; ON: outside nabkha. PRA-protease (mg Tyr kg^{-1} soil h^{-1}); POA-polyphenol oxidase (mmol kg^{-1} soil h^{-1}); UA-urease (mg NH_4^+-N kg^{-1} soil h^{-1}); PHA-phosphomonoesterase (mg kg^{-1} soil h^{-1}); DHA-dehydrogenas (mg TPF kg^{-1} soil h^{-1}).

3.2. Soil enzymatic activities

The activities of soil protease, phosphomonoesterase, urease, polyphenol oxidase, and dehydrogenase at different soil depths (0–10, 10–20, and 20–30 cm) in WN, UC, and ON are shown in Table 4. Based on the three-way ANOVA results ($P < 0.01$), significant differences in the activities of these enzymes existed among species, among the three microsites, and with soil depths (Table 3). Similar with those in soil nutrients, the activities of soil protease, phosphomonoesterase, urease, polyphenol oxidase, and dehydrogenase in the three nebkhas were all higher in the IN site and in the topsoil (0–10 cm). Moreover, values significantly decreased with increased distance from the nebkha and with soil depth, i.e., WN > UC > ON, 0–10 cm > 10–20 cm > 20–30 cm. The WN/ON of soil protease, phosphomonoesterase, urease, polyphenol oxidase, and dehydrogenase activities in the 0–10 cm depth in WN, UC, and ON were 1.22–2.32, 1.74–4.19, 1.98–2.53, 1.01–1.67, and 1.69–1.80, respectively, and the enrichment ratios of average activities in the 0–30 cm depth were 1.24–3.14, 2.02–3.50, 1.70–1.91, 1.09–1.22, and 1.31–1.44, respectively. The enzyme activities in different microsites varied depending on the enzyme and shrub species. For example, significant differences in phosphomonoesterase activities were found in all microsites of the three shrub lands. However, urease activity was significantly different only in the *C. microphylla* site.

3.3. Microbial community metabolic profiles

Microbial CLPP in WN, UC, and ON at 0–10 cm soil depth was assessed using Biolog Ecoplates, and the results are shown in Fig. 1. During the first 24 h, the AWCD of all samples were almost the same at the lower level. After 24 h, values rapidly increased with time, and approximately sigmoidal curves were formed at the end of incubation. At each measuring point (24–168 h), the AWCD values of each shrub species were observed in the following order: WN > UC > ON. Biolog Ecoplate includes six groups of carbon substrates, i.e., polymers, phenols, carboxylic acids, amino acid, and amines. Significant differences in AWCD of carbon substrates except for carboxylic acids in *C. microphylla* and carbohydrates in *S. gordejevii* were found among the microsites, indicating higher microbial metabolic function in WN and UC soils (Fig. 2). The changes in the AWCD of single group of carbon substrate in WN, UC, and ON were consistent with those of the total AWCD of each shrub species.

3.4. Correlation between soil microbiological properties and nutrients

Correlation coefficients among soil pH, nutrients (organic matter; total N and P; and available N, P, and K), enzymatic activities (protease, polyphenol oxidase, urease, phosphomonoesterase, and dehydrogenase), and total AWCD are shown in Table 5. Soil organic matter; total N and P; and available N, P, and K were significantly and positively correlated to soil protease, polyphenol oxidase, urease, phosphomonoesterase, and dehydrogenase (except for correlations between available P and polyphenol oxidase, and between total N and dehydrogenase), respectively. Significant correlations were also observed among soil nutrients and among enzymes (except for the correlations between protease and polyphenol oxidase and between dehydrogenase and polyphenol oxidase). AWCD was significantly and positively correlated to soil nutrient contents, soil protease, phosphomonoesterase, and dehydrogenase activities. No significant correlations were found between soil pH and available N, phosphomonoesterase, dehydrogenase, and AWCD.

4. Discussion

Shrubs control the distribution of soil nutrients, the activities of soil organisms, and the evolution of soil physicochemical properties in desertified soil (Wezel et al., 2000; Titus et al., 2002; Housman et al., 2007; Liu et al., 2011). Our results confirmed that nebkhas formed by *C. microphylla*, *A. manshurica*, and *S. gordejevii* in the Horqin Sandy Land accumulated soil nutrients (soil organic matter; total N and P; available N, P, and K), which gradually developed into fertile islands in contrast to the open areas, thereby inducing spatially heterogeneous distributions of soil nutrients. The degree

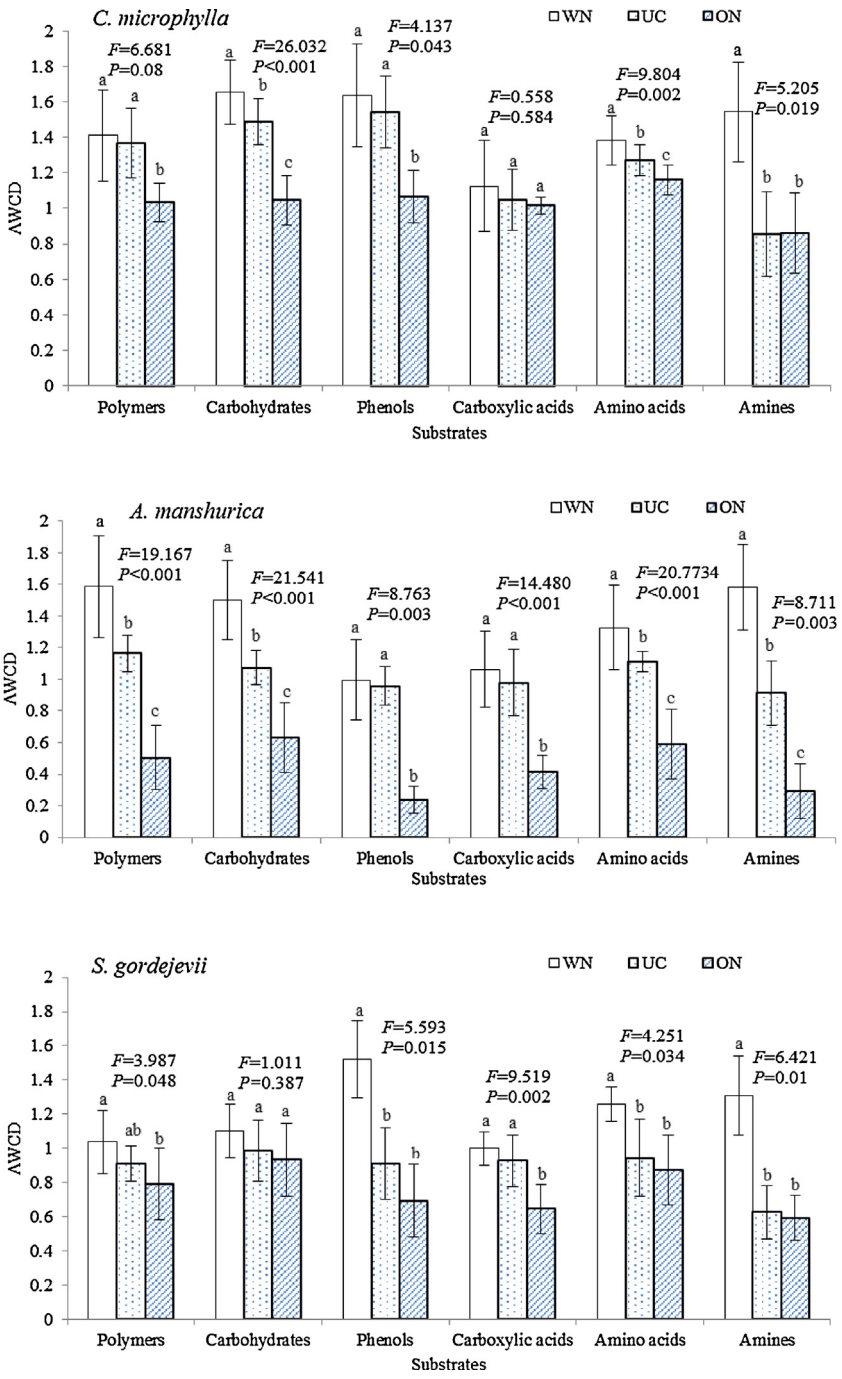

Fig. 2. Categorized substrate utilization pattern of soils using Biolog Ecoplate for average well color development (AWCD) (based on the 96 h data) in WN, UC, and ON. Bars with the same letter denote no significant difference. Data were generated by four replicates. WN: within nabkha; UC: under crown; ON: outside nabkha.

of soil nutrient enrichment varied among nebkha types. This finding is consistent with the results of Li et al. (2008), Abril et al. (2009), Yang et al. (2011), Zhang et al. (2011), and Li et al. (2014). Studies have demonstrated that abiotic factors (e.g., uneven rainfall, alluvial process, and topography) and biotic factors (e.g., grazing by ungulate herbivores, plant community structure, and coexistence of plant species) create spatial heterogeneity in soil properties in a variety of ecosystems (Kleb and Wilson, 1997; Fisk et al., 1998; Burke et al., 1999; Augustine and Frank, 2001; Kelly and Burke, 2001). Potential mechanisms by which shrub nebkhas modify heterogeneity of soil property relative to windy–sandy land include (1) differences in plant growth forms, genera, and species, including the process of mineral nutrition uptake, aboveground biomass, tissue allocation, and root architecture patterns (Schenk and Jackson, 2002); (2) re-distribution patterns of soil resource by shrub and hence alterations in inputs to the soil by litter and root secretions (Augustine and Frank, 2001); (3) long-term effects of plant community composition on spatial and temporal distributions of the quantity and quality of leaf and stem litter that are related to decomposition rate of litter due to the pronounced effect of nebkhas on plant community structure (Pastor et al., 1998, El-Bana et al., 2002); (4) interactions with small mammal or insect such as burrowing cave/nest and inputs of dung and urine, which in turn influences heterogeneity of soil property (Augustine and Frank, 2001); (5) higher rates of aeolian dust deposition functioning as natural barrier reducing wind velocity, which consequently

Table 5
Correlation coefficients among soil pH, nutrient, enzymatic activity, and AWCD.

Item	SOM	TP	AVP	TN	AVN	AVK	pH	PRA	POA	UA	PHA	DHA	AWCD
SOM	1												
TP	0.802**	1											
AVP	0.479*	0.415**	1										
TN	0.849**	0.778**	0.502**	1									
AVN	0.640**	0.427*	0.419*	0.564**	1								
AVK	0.462*	0.527**	0.340*	0.396*	0.390*	1							
pH	0.372*	0.475**	0.329*	0.442*	−0.117	0.286*	1						
PRA	0.543**	0.528**	0.630**	0.564**	0.493**	0.399*	0.339*	1					
POA	0.359*	0.427**	0.199	0.327*	0.018	0.445**	0.562**	0.134	1				
UA	0.575**	0.523**	0.325*	0.471**	0.249*	0.483**	0.317*	0.364*	0.356*	1			
PHA	0.816**	0.666**	0.476**	0.704**	0.671**	0.499**	0.206	0.614**	0.272*	0.612**	1		
DHA	0.244*	0.230*	0.371*	0.143	0.562**	0.485**	−0.169	0.448**	−0.059	0.251*	0.355*	1	
AWCD	0.523**	0.326*	0.306*	0.347*	0.625**	0.316*	−0.158	0.476*	−0.325	0.083	0.462*	0.455*	1

SOM-soil organic matter; TP-total P; AVP-available P; TN-total N; AVN-available N; AVK-available K; PRA-protease; POA-polyphenol oxidase; UA-urease; PHA-phosphomonoesterase; DHA-dehydrogenas.

* $P < 0.05$.

** $P < 0.01$; $n = 108$.

collects wind-blown fine materials by entrapment and deposition of dust through stemflow and throughfall (Cao et al., 2000, 2011; Su and Zhao, 2003; Zhang et al., 2004; Zhao et al., 2007); and (6) micro-environmental conditions created by nebkhas (e.g., soil temperature, soil moisture, soil porosity, and illumination), which affect the decomposition rate of litter, nutrient cycle, and invasion of herbaceous plants (El-Bana et al., 2002, 2003).

Our results also showed that enrichment of soil nutrients induced by nebkhas varied with nutrient type and shrub species. The average enrichment rates (in 0–30 cm depth) of soil organic matter, available N, and available P were considerably higher compared with those of the other soil nutrients, suggesting that nebkhas increased the availability of soil nutrients. In addition, the organic matter; total N and P; and available N, P, and K of the analyzed soils all deceased with soil depth, which is consistent with reported results (Reynolds et al., 1999; Li et al., 2008; Cao et al., 2011). Our results indicated that topsoils beneath the shrub crown and within and outside nebkhas were all more fertile than those in deeper depths probably because of more litter inputs, lower rate of soil wind erosion, and more aeolian dust deposition of the former (Zhang et al., 2004; Zhao et al., 2007; Cao et al., 2011). Among the three shrub species, *C. microphylla* nebkha showed the greatest ability in accumulating nutrients, particularly available N and P, compared with those of *A. manshurica* and *S. gordejevii* nebkhas. These results confirmed our hypotheses that islands of fertility effect varies among the shrub nebkha types.

Enzymatic activities are considered indices of soil microbiological properties and soil fertility (Badiane et al., 2001) and are commonly used to evaluate the effects of land conversion, drought, salinization, and other human activities on soil quality (Sardans and Peñuelas, 2005; Cao et al., 2011; Pan et al., 2013; Zhang et al., 2015), which is very sensitive to environmental changes. In this study, the activities of soil polyphenol oxidase, phosphomonoesterase, dehydrogenase, urease, and protease showed decreasing trend with soil depth and distance from the center of nebkha, similar with those of soil nutrients. Meanwhile, significant positive correlations between soil nutrients and enzymes were found, confirming previous observations (Cao et al., 2008, 2011). Decrease in soil enzyme activities with increasing soil depth was observed in agricultural, grassland, and forest soils when litter and other organic matter accumulated on the soil surface (Aon et al., 2001; Taylor et al., 2002; Cao et al., 2008). One important factor that accounts for the higher soil enzymatic activities within nebkha and in the topsoil is the asymmetrical organic matter input through the soil profile (Cao et al., 2011). Another important factor is improved soil aeration resulting from increased soil porosity, thereby increasing soil O_2 supply. Improved O_2 availability further influenced the growth and metabolism of soil microbial community and hence enzyme secretion. Additionally, arid ecosystem effectively traps water and thus preserves and increases soil moisture and plant biodiversity, which probably facilitated the increase in soil enzymatic activities (El-Bana et al., 2002).

Recently, studies used the Biolog microplate technique to differentiate functional diversity of soil microflora from different habitats (Crecchio et al., 2004; Plassart et al., 2008; Huang et al., 2012; Zhang et al., 2015), because the method reveals the CLPPs for carbon source utilization of soil microflora (Zak et al., 1994). In our study, results of Biolog Ecoplates culture reflected the differences in the potential carbon metabolic function of soil microflora among the microenvironments. The trend in substrate utilization level (AWCD) was consistent with those in soil nutrients and enzymatic activities, confirming the close relationships among soil microbes, enzyme activity, and soil nutrient content (Table 5).

5. Conclusions

C. microphylla, *A. manshurica*, and *S. gordejevii* nebkhas are the major sources of soil nutrient and heterogeneity of microbiological property in the Horqin Sandy Land semi-arid ecosystem. Fertile islands are formed within nebkhas and under the canopy, whose effects differ among nebkha types induced by different shrub species. Phytogenic nebkhas trap and preserve soil nutrients and increase soil enzymatic activities and functional diversity for carbon source utilization of soil microflora. The results of this study contribute to the better understanding of function of desert phytogenic nebkhas, and the appropriate management and conservation of nebkhas should be emphasized in the ecological restoration of arid or semi-arid fragile ecosystems.

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