

N and P resorption in a pioneer shrub (*Artemisia halodendron*) inhabiting severely desertified lands of Northern China

YuLin LI*, Chen JING, Wei MAO, Duo CUI, XinYuan WANG, XueYong ZHAO

Naiman Desertification Research Station, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China

Abstract: Nutrient resorption is an important conservation mechanism for plants to overcome nutrient limitation in the less fertile area of desertified land. In the semi-arid Horqin Sandy Land of Northern China, the shrub *Artemisia halodendron* usually colonizes into the bare ground of severely desertified land as a pioneer species. It is, therefore, expected that *A. halodendron* will be less dependent on current nutrient uptake through efficient and proficient resorption of nutrients. In this study, we found that averaged nitrogen (N) and phosphorus (P) concentrations in senesced leaves significantly varied from 12.3 and 1.2 mg/g in the shifting sand dune to 15.9 and 1.9 mg/g in the fixed sand dune, respectively, suggesting that foliar N and P resorption of *A. halodendron* were more proficient in the shifting sand dune. In particular, positive relationships between nutrient concentrations in senesced leaves and soil nutrient availability indicate that *A. halodendron* in infertile habitats is more likely to manage with a low level of nutrients in senesced leaves, giving this species an advantage in infertile soil. Moreover, foliar N- and P-resorption efficiencies and proficiencies showed limited inter-annual variability although annual precipitation varied greatly among 2007–2009. However, N and P resorption of *A. halodendron* were not more efficient and proficient than those previously reported for other shrubs, indicating that the pioneer shrub in sand dune environments does not rely more heavily than other plants on the process of resorption to conserve nutrients. Incomplete resorption of nutrients in *A. halodendron* suggests that senesced-leaf fall would return litter with high quality to the soil, and thereby would indirectly improve soil nutrient availability. The restoration of desertified land, therefore, may be accelerated after *A. halodendron* pioneers into shifting sand dunes.

Keywords: foliar nutrient concentration; nutrient-resorption efficiency; nutrient-resorption proficiency; senesced vs. green leaves; desertification; soil nutrient availability

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Land desertification, a human-induced land degradation process, is one of the most serious environmental and socioeconomic issues (Lal, 2000; Wang, 2000), and has resulted in large areas of shifting sand lands with bare sandy soils in the semi-arid regions of Northern China. The bare sandy soil is generally low in soil nutrients and tends to inhibit the establishment of new seedlings as well as the growth of herbaceous plants (Liu et al., 1996; Yan and Liu, 2010). However,

there are some common perennial shrubs which are able to pioneer by growing in the less fertile bare sandy areas in North China (Zhao et al., 2007). These plant species, with an ability of invading bare sandy areas, must possess some kind of strategies adapting to poor soil nutrient availability, especially when sufficient soil moisture is available (Su et al., 2005).

Withdrawal of nutrient before leaf death and abscission is one of the strategies employed by plants to

*Corresponding author: YuLin LI (E-mail: lyulin@gmail.com)

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overcome nutrient limitation in nutrient-poor ecosystems (Aerts, 1996; Yuan and Chen, 2009). Nutrient resorption, quantified by nutrient-resorption efficiency (the proportion of nutrient resorbed from senesced leaves) or nutrient-resorption proficiency (the level to which nutrient concentration is reduced in senesced leaves), allows leaf nutrients to be reused rather than lost with leaf fall, and thus facilitates plant growth, reproduction, and competitive ability (May and Killingbeck, 1992), especially in nutrient-poor environments, where the annual nutrient requirement of perennials is strongly dependent on resorption from senescing tissues (Aerts et al., 2007; Lu et al., 2012). Some evidences suggested that desert shrubs rely more heavily than other plants on the process of resorption to conserve nitrogen (N) and phosphorus (P) (Killingbeck, 1993a). It is, therefore, expected that plants pioneering in the less fertile bare sandy areas of desertified land may considerably resorb foliar nutrients to increase plant fitness. However, this hypothesis remains uncertain because high nutrient-use efficiency (Lajtha, 1987), low growth rate, long green tissue life span (Aerts and Chapin III, 2000), and tight nutrient recycling (Carrera et al., 2000) are regarded as possible strategies contributing to nutrient conservation in many desert perennials.

Nutrient availability in soils is thought to be a determining factor in nutrient resorption patterns in plant species (Killingbeck, 1993b; Gusewell, 2005; Huang et al., 2008). Previous studies demonstrated that nutrient-resorption efficiency of plant species significantly decreased with increasing soil nutrient availability (Yuan et al., 2005a; Huang et al., 2008). However, some reports suggested that high nutrient-resorption efficiency is not an important adaptation to low soil nutrient status, but a characteristic of most plant species (Chapin and Kedrowski, 1983). Aerts (1996) also claimed that there were no clear nutritional controls on nutrient-resorption efficiency. In contrast, nutrient-resorption proficiency patterns show a stronger relation to soil fertility, with the highest proficiency at infertile sites (Killingbeck, 1996). In addition, other factors that have an effect on nutrient resorption include soil water availability and climate (air and soil temperature, wind, precipitation,

etc.). Therefore, Killingbeck (1996) suggested that it is essential to measure nutrient resorption for several years to determine the capacity of a particular plant species to retranslocate nutrients. Some studies have already demonstrated that nutrient resorption varied greatly within plant species and sites among different years (Nordell and Karlsson, 1995; Killingbeck, 1996; Drenovsky et al., 2010), indicating that environmental effects have a greater impact on nutrient resorption than genetic factors. However, multi-year observation of nutrient resorption is still limited. For example, only about 5% of the recent meta-analyses of senesced-leaf nutrient concentrations had more than one year of resorption data (Yuan and Chen, 2009).

In the severely desertified areas of Horqin Sandy Land, North China, a native shrub *Artemisia halodendron* usually colonizes into bare sandy soils as a pioneer plant (Liu et al., 1996). Colonization of *A. halodendron* firstly improves soil nutrient availability and thereby promotes restorative succession in shifting sand land (Su et al., 2005; Zhao et al., 2007). As a result, shifting sand land gradually evolves into semi-fixed or fixed sand land. Apparently, there is a distinct increasing gradient of soil nutrient availability along shifting, semi-fixed and fixed sand lands (Chen et al., 2009). In this paper, we reported the results of a field study in which we examined leaf nutrient resorption of *A. halodendron* inhabiting shifting, semi-fixed and fixed sand dune habitats during the three consecutive years (2007–2009) in Horqin Sandy Land, North China. We focused on N and P, as these nutrients are the major limiting nutrients in sand lands. Since *A. halodendron* could colonize into infertile bare sandy soils, we hypothesized that foliar N and P in *A. halodendron* would be more efficiently and proficiently resorbed relative to other plants. Further, considering the differences in nutrient availability among the three habitats, we also hypothesized that higher N- and P-resorption efficiencies and proficiencies of *A. halodendron* would be observed in infertile habitats such as the shifting sand dune, but lower N- and P-resorption efficiencies and proficiencies in relatively fertile habitats such as the fixed sand dune. Last, we predicted that during the three consecutive years, nutrient resorption would significantly vary as cli-

matic conditions would influence the capacity of plant species to retranslocate nutrients.

1 Materials and methods

1.1 Study site

The study was carried out at Naiman Desertification Research Station (42°58'N and 120°43'E, 345 m asl) of Chinese Ecosystem Research Network (CERN), eastern Inner Mongolia, China, located at the south-west of Horqin Sandy Land, in a zone of continental semi-arid monsoon climate. The annual mean air temperature is about 6.4°C, and the coldest and warmest monthly mean temperatures are −13.1°C recorded in January and 23.7°C in July, respectively. The mean annual accumulated air temperature above 10°C ranges from 3,000 to 3,400°C. The frost-free period is 137–150 days per year. The mean annual precipitation is 362 mm, nearly 70% of which falls from June through August. The mean annual pan evaporation is 2,000 mm. Prevailing wind directions are northwest in winter and spring, and southwest to south in summer and autumn. The annual mean wind speed ranges from 3.4 to 4.1 m/s.

In this area, the geomorphologic landscape is characterized by sand dunes alternating with gently undulating interdune lowlands. The soils are very infertile and sandy with light yellow color, coarse texture and loose structure. Sand dunes in this area are generally classified into three main forms according to vegetation cover and area of shifting sand: fixed or stabilized, semi-fixed or semi-stabilized, and shifting or unstabilized (Zhu et al., 1989). Vegetation is characterized by the shrubland of *A. halodendron* with scattered trees and windbreak tree belt of *Populus* spp. The dominant plant species include *A. halodendron*, *Caragana microphylla*, *Artemisia scoparia*, *Setaria viridis*, and *Salix gordejewii* (Liu et al., 2009).

The study was conducted during growing seasons (April–October) of 2007, 2008, and 2009. Total annual precipitation at Naiman Desertification Research Station was 326.6 mm (2007), 244.0 mm (2008), and 257.1 mm (2009), nearly 89.7%, 86.8%, and 94.4% of which, respectively, falls in growing seasons during the study period (Fig. 1). Annual mean air temperature was 8.0, 7.7,

and 6.8°C, during 2007, 2008, and 2009, respectively.

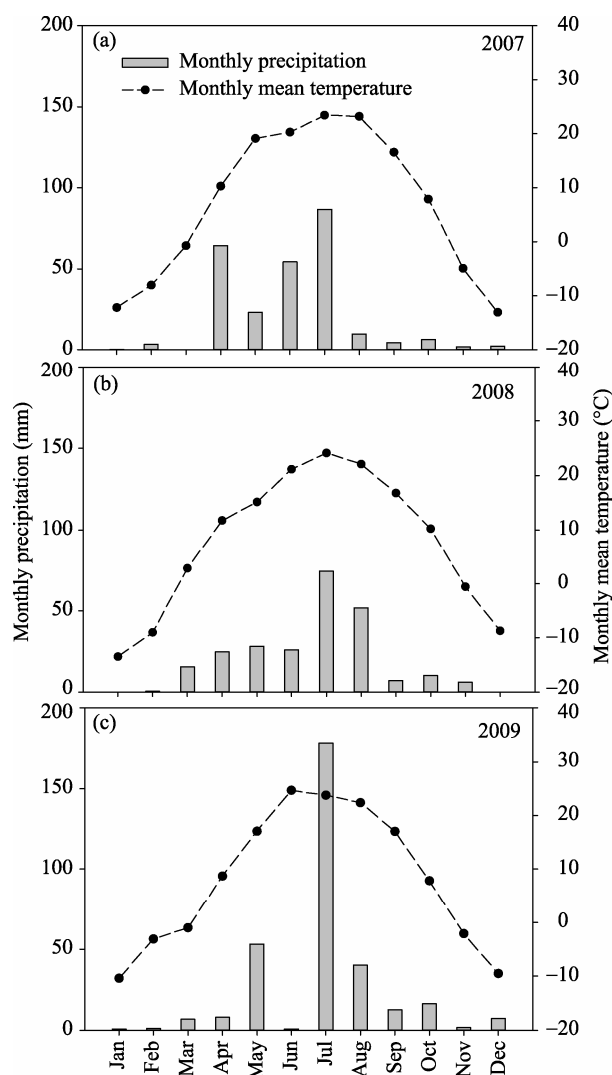


Fig. 1 Monthly precipitation and monthly mean temperature and of three sampling years in Horqin Sandy Land

1.2 Leaf and soil sampling

Field investigation was performed in a shrubland of *A. halodendron* with an area of about 35 hm², where large domestic herbivores were excluded to restore vegetation. We selected three typical kinds of habitats (i.e. shifting sand dune, semi-fixed sand dune, and fixed sand dune) in this shrubland, each with 3 replications for the nutrient resorption study. In the 3 replications of each habitat, we randomly marked 15 healthy, fully sunlit individuals (usually 5 individuals in each replication) of *A. halodendron* to collect leaf and soil samples. In every July during 2007, 2008, and 2009, 150–200 fully sunlit mature green leaves were

randomly collected from each marked individual, meanwhile a soil sample was taken under the canopy of the shrub using a 5-cm diameter soil auger at the 0–20 cm soil layer. In autumn (late September to early October), similar collections were made for senesced leaves on the same individuals. The leaves of a single shrub and soil sample under its canopy represented one sample unit. In total, we got 15 pairs of leaf and soil samples in each habitat. Leaves with obvious signs of herbivory, galls, and fungal attack were not sampled. Leaves that were clearly very thin (shaded canopy position) were also avoided. Senesced leaves were collected as dead leaves that were ready to abscise. We considered leaves ready to abscise if they were completely dry yellow without signs of deterioration (Norby et al., 2000; Wright and Westoby, 2003). These leaves were easily identified as they are generally a different colour from live leaves (often yellow), and can be removed by a gentle flicking of the branch or leaf. Green and senesced leaf samples were immediately taken to the laboratory, and then oven-dried at 60°C to constant weight and kept dry until analyses.

1.3 Leaf and soil chemistry analyses

All leaf samples were ground using a centrifugal mill (Cyclotec Sample Mill; Tecator, Höganäs, Sweden) to obtain a uniform particle size of <1 mm. N concentrations of green and senesced leaves were analyzed colorimetrically by Kjeldahl acid-digestion method (UDK140 Automatic Steam Distilling Unit, Automatic Titroline 96, Italy). For P measurements, 2 ml of 36 N H₂SO₄ and 3 ml of H₂O₂ were added to a 20 mg sample of leaf material and heated at 360°C for 4 h. After this mineralization step, P concentration was measured colorimetrically with an autoanalyser (Evolution II; Alliance Instruments, Frépillon, France) using the molybdenum blue method (Grimshaw et al., 1989).

After the soil samples were brought to the laboratory, part of each soil sample was kept in 0–4°C refrigerator to analyze inorganic nitrogen (NH₄⁺-N and NO₃⁻-N). The rest was air-dried, then ground and passed through a 0.25-mm sieve for carbon (C), N and P analysis. Soil organic C was determined by dichromate oxidation of Walkley-Black (Nelson and Sommers, 1982), and soil total N and total P were analyzed following the same procedure with leaf N and

P measurements. The Olsen sodium bicarbonate method was used to measure soil available P. Inorganic N (NH₄⁺-N and NO₃⁻-N) was measured by using colorimetric method with fresh soil samples after extraction with 2 M KCl.

1.4 Data analysis

N and P concentrations in green and senesced leaves were used to calculate N-resorption efficiency (NRE) and P-resorption efficiency (PRE) on a mass basis (Killingbeck, 1996).

$$NRE = [(N_{\text{green}} - N_{\text{sen}}) / N_{\text{green}}] \times 100\%, \quad (1)$$

$$PRE = [(P_{\text{green}} - P_{\text{sen}}) / P_{\text{green}}] \times 100\%. \quad (2)$$

Where N_{green} and N_{sen} represent N concentration in the green leaves and senesced leaves, respectively; and P_{green} and P_{sen} represent P concentration in the green leaves and senesced leaves, respectively. The nutrient concentrations in senesced leaves were considered a direct indicator of nutrient-resorption proficiency, which is defined as the absolute level to which N is reduced in senesced leaves (Killingbeck, 1996).

We employed ANOVA with repeated measures to test the difference in leaf N and P concentrations, and soil properties among different habitats and different sampling years. Habitat was set as the between-subject factor with sampling years as the within-subject variables. The data were transformed logarithmically if the assumptions of normality and homogeneity were violated during analysis. Main effects and interactions were tested for significance using the appropriate error terms as determined by the expected mean square. If the difference was significant, post-hoc multiple comparisons were subsequently made using Turkey HSD test. Single linear regressions were used to test the power of soil available N and P of three sampling years under shrub canopies (within and among habitats) to predict green and senesced leaf N and P, and NRE and PRE of individual shrubs (across three sampling years). Statistical analysis was performed using SPSS 16.0 for windows.

2 Results

There were significant differences ($P < 0.001$) in organic C, total N, available N, total P, and available P of soils at the 0–20 cm depth among the three habitats

(Table 1). All soil nutrients were the lowest in the shifting sand dune, intermediate in the semi-fixed sand dune, and the highest in the fixed sand dune ($P<0.05$; Table 1). Averaged soil organic C, total N and total P at the 0–20 cm depth in the fixed sand dune increased by 1.07, 0.83 and 1.11 folds, respectively, relative to the shifting sand dune. Available N and P followed the same pattern, with respective 1.04-

and 0.41-fold increases in the soil of the fixed sand dune relative to the shifting sand dune (Table 2), suggesting that soil nutrient availability was considerably improved in the fixed sand dune. However, no significant inter-annual differences were detected for soil properties from the three habitats (Table 1).

Nearly 48% of foliar N in *A. halodendron* was re-sorbed during leaf senescence in the three habitats

Table 1 Soil properties (0–20 cm depth) in the fixed sand dune, semi-fixed sand dune, and shifting sand dune during 2007–2009 in Horqin Sandy Land of northern China (means \pm SE, $n=3$)

Soil property	Year	Fixed sand dune	Semi-fixed sand dune	Shifting sand dune
Soil organic C (g/kg)	2007	2.89 \pm 0.22 ^a	2.10 \pm 0.11 ^b	1.46 \pm 0.16 ^c
	2008	2.92 \pm 0.21 ^a	2.09 \pm 0.10 ^b	1.36 \pm 0.14 ^c
	2009	3.13 \pm 0.11 ^a	2.23 \pm 0.12 ^b	1.48 \pm 0.09 ^c
Soil total N (g/kg)	2007	0.24 \pm 0.02 ^a	0.17 \pm 0.02 ^b	0.14 \pm 0.02 ^b
	2008	0.24 \pm 0.02 ^a	0.18 \pm 0.01 ^b	0.12 \pm 0.01 ^c
	2009	0.26 \pm 0.02 ^a	0.19 \pm 0.01 ^b	0.14 \pm 0.01 ^c
Soil available N (mg/kg)	2007	5.74 \pm 0.34 ^a	3.55 \pm 0.31 ^b	2.97 \pm 0.32 ^b
	2008	5.52 \pm 0.22 ^a	3.48 \pm 0.29 ^{ab}	2.62 \pm 0.26 ^b
	2009	6.09 \pm 0.39 ^a	3.74 \pm 0.31 ^b	2.92 \pm 0.35 ^b
Soil total P (g/kg)	2007	0.14 \pm 0.01 ^a	0.09 \pm 0.00 ^b	0.06 \pm 0.00 ^c
	2008	0.13 \pm 0.01 ^a	0.10 \pm 0.01 ^b	0.07 \pm 0.01 ^b
	2009	0.14 \pm 0.01 ^a	0.09 \pm 0.01 ^b	0.07 \pm 0.01 ^b
Soil available P (mg/kg)	2007	2.26 \pm 0.10 ^a	1.87 \pm 0.12 ^b	1.62 \pm 0.06 ^b
	2008	2.31 \pm 0.11 ^a	1.70 \pm 0.13 ^b	1.67 \pm 0.08 ^b
	2009	2.41 \pm 0.12 ^a	1.74 \pm 0.12 ^b	1.64 \pm 0.08 ^b

Note: Values followed by different letters in rows mean significant differences at the 0.05 level.

Table 2 ANOVA with repeated measures for effects of habitats and sampling years on soil properties

Soil property	Source of variation	df	Ms	F	P
Soil organic C (g/kg)	Habitat	2	26.850	35.42	<0.001
	Year	2	0.315	2.46	0.092
	Habitat \times year	4	0.051	0.40	0.812
Soil total N (g/kg)	Habitat	2	0.143	26.75	<0.001
	Year	2	0.003	1.30	0.278
	Habitat \times year	4	0.001	0.49	0.741
Soil available N (mg/kg)	Habitat	2	105.690	28.31	<0.001
	Year	2	1.610	4.64	0.012
	Habitat \times year	4	0.220	0.64	0.633
Soil total P (g/kg)	Habitat	2	0.065	23.39	<0.001
	Year	2	<0.001	0.33	0.719
	Habitat \times year	4	<0.001	0.95	0.441
Soil available P (mg/kg)	Habitat	2	5.870	14.32	<0.001
	Year	2	0.017	0.44	0.645
	Habitat \times year	4	0.100	2.70	0.036

over three sampling years of the study. Mean NRE of *A. halodendron* did not vary significantly among the three habitats, but mean foliar N concentrations in green and senesced leaves were significantly higher in the fixed sand dune than in the shifting sand dune (Table 3 and Fig. 2). Mean N concentrations in green leaves varied between 23.4 ± 1.3 mg/g in the shifting sand dune in 2008 and 29.2 ± 1.0 mg/g in the fixed sand dune in 2009. Meanwhile, mean N concentration in senesced leaves, indicator of N-resorption proficiency (NRP), significantly increased ($P < 0.01$) by 21% in the fixed sand dune relative to the shifting sand dune. In other words, it suggested that NRP significantly decreased with soil nutrient availability across the three habitats. Patterns of inter-annual variations of green-leaf N concentration, senesced-leaf N concentration, and NRE were similar across the three habitats (Fig. 2). Moreover, no significant effects were detected in green- and senesced-leaf N concentrations and NRE among the three sampling years (Table 3).

In contrast to NRE, PRE in *A. halodendron* was more efficient, with averaged value near to 57% in the

three habitats over three sampling years of the study. There was no significant variation of PRE among the three habitats (Fig. 2). However, mean P concentrations in green and senesced leaves significantly increased from 3.1 ± 0.15 and 1.2 ± 0.07 mg/g in the shifting sand dune to 4.3 ± 0.2 and 1.9 ± 0.1 mg/g in the fixed sand dune, respectively. Similar to N, green- and senesced-leaf P concentrations and PRE also did not differ significantly among three sampling years (Table 3).

N concentrations in green and senesced leaves of individual shrubs were positively related to soil available N under the shrub canopy within or among different habitats across the three sampling years (Fig. 3), suggesting that NRP decreased with increases of soil available N. In contrast, NRE was generally unrelated to soil available N within or among different habitats across the three sampling years. Similar relationships were displayed between leaf P concentrations and soil available P, and similar to NRE, PRE also did not show any relations to soil available P within or among different habitats across the three sampling years.

Table 3 ANOVA with repeated measures for effects of habitats and sampling years on foliar nutrient concentrations and nutrient-resorption efficiencies

	Source of variation	df	Ms	F	P
Green-leaf N concentration (mg/g)	Habitat	2	279.00	8.03	0.001
	Year	2	17.39	1.51	0.227
	Habitat×year	4	0.42	0.04	0.997
Senesced-leaf N concentration (mg/g)	Habitat	2	101.40	7.88	0.001
	Year	2	6.16	1.52	0.224
	Habitat×year	4	1.02	0.25	0.908
N-resorption efficiency (NRE; %)	Habitat	2	33.75	1.10	0.343
	Year	2	22.48	1.01	0.370
	Habitat×year	4	12.53	0.56	0.690
Green-leaf P concentration (mg/g)	Habitat	2	9.66	11.63	<0.001
	Year	2	0.18	1.20	0.307
	Habitat×year	4	0.22	1.41	0.238
Senesced-leaf P concentration (mg/g)	Habitat	2	2.73	8.22	0.001
	Year	2	0.14	2.72	0.720
	Habitat×year	4	0.06	1.13	0.340
P-resorption efficiency (PRE; %)	Habitat	2	102.40	1.54	0.227
	Year	2	55.06	2.16	0.122
	Habitat×year	4	8.24	0.32	0.862

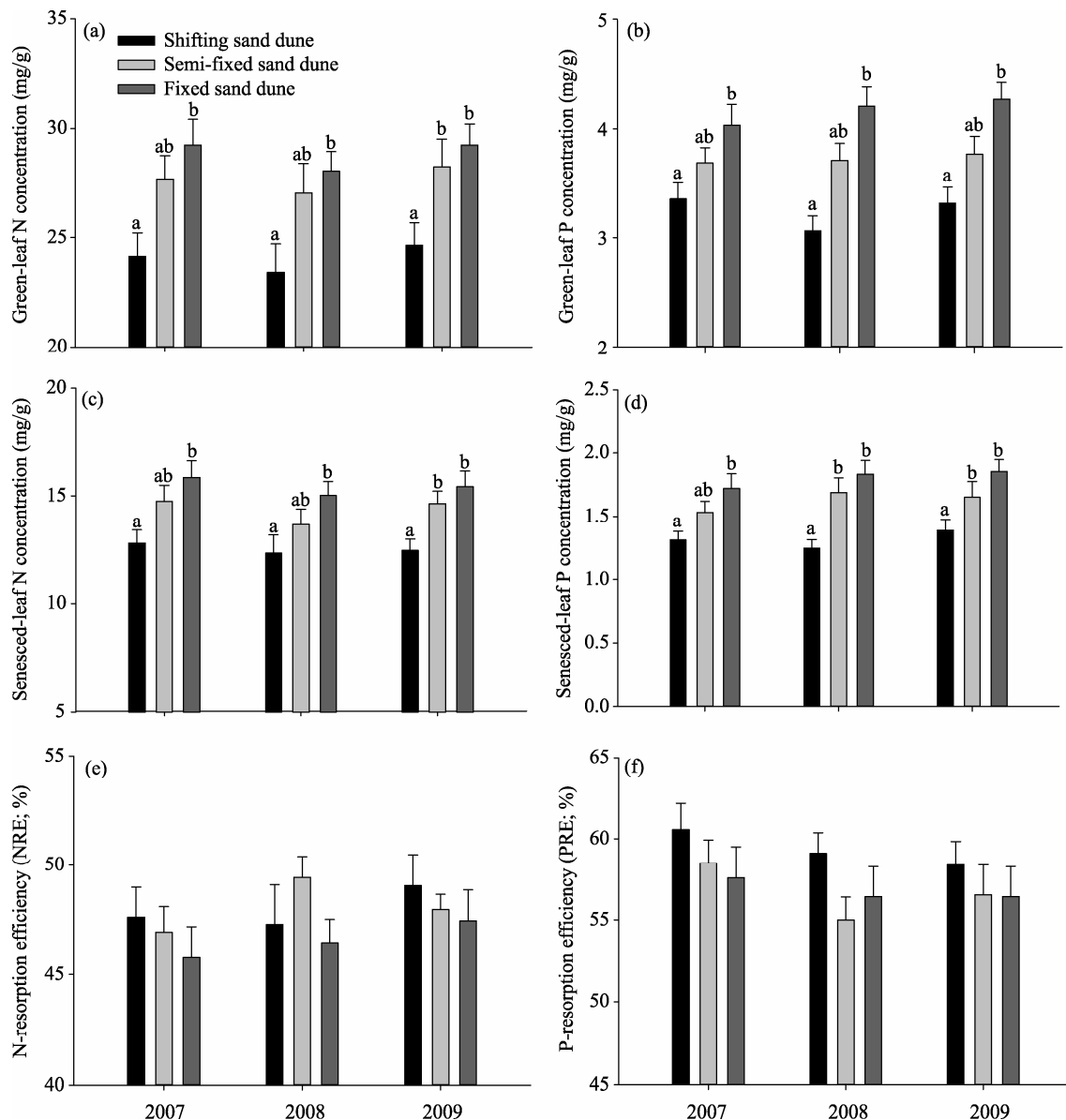


Fig. 2 Leaf N and P concentrations and resorption efficiencies of *Artemisia halodendron* in three habitats of three sampling years (means \pm SE, $n=3$). Significant differences among different habitats are indicated by different letters (Turkey's test, $P=0.05$).

3 Discussion

3.1 Nutrient resorption in *A. halodendron*

Deciduous plants appear to have ability to resorb 50% or more of foliar N and P during leaf senescence (Luyssaert et al., 2005; Yuan and Chen, 2009). Aerts (1996) listed averaged 54% of N resorption efficiency for 115 deciduous trees and averaged 50% of P resorption efficiency for 98 deciduous trees and shrubs. In addition, averaged 53% of N resorption efficiency for shrub species was also reported in a sand land en-

vironment in North China (Yuan et al., 2005b). Contrary to our first hypothesis, we found that foliar N resorption of pioneer shrub *A. halodendron* was not more efficient (averaged resorption efficiency of 47%), even in the shifting sand dune (averaged resorption efficiency of 48%), than those previously reported for other trees and shrubs (Aerts, 1996; Yuan et al., 2005b), although P was relatively more efficiently resorbed during leaf senescence, with an averaged resorption efficiency of 57% in sand dune environments. This suggests that nutrient resorption, especially foliar N, is not served as the major strategy to

increase plant fitness of pioneer shrub *A. halodendron* in the bare sandy soil in Horqin Sandy Land. It should be mentioned that we might have eventually underestimated nutrient-resorption efficiency, due to probable changes in specific leaf mass resulting from resorption of soluble carbon compounds (Aerts, 1996). It has been suggested that estimates of proportional N resorption made on the basis of leaf area may be more accurate than those made on the basis of leaf mass (Luyssaert et al., 2005). However, leaf area shrinkage also may occur during senescence and eventually un-

derestimate resorption efficiency (van Heerwaarden et al., 2003). Especially for *A. halodendron*, leaves shrunk remarkably during leaf senescence according to our field investigation. Therefore, mass-based NRE data were still used in this study.

Resorption proficiency is considered to be a nutrient conservation trait influenced by natural selection, and it is useful in describing the terminal nutrient level in plants during senescence (Killingbeck, 1996; van Heerwaarden et al., 2003; Richardson et al., 2005). The mean N concentration in the senesced leaves of

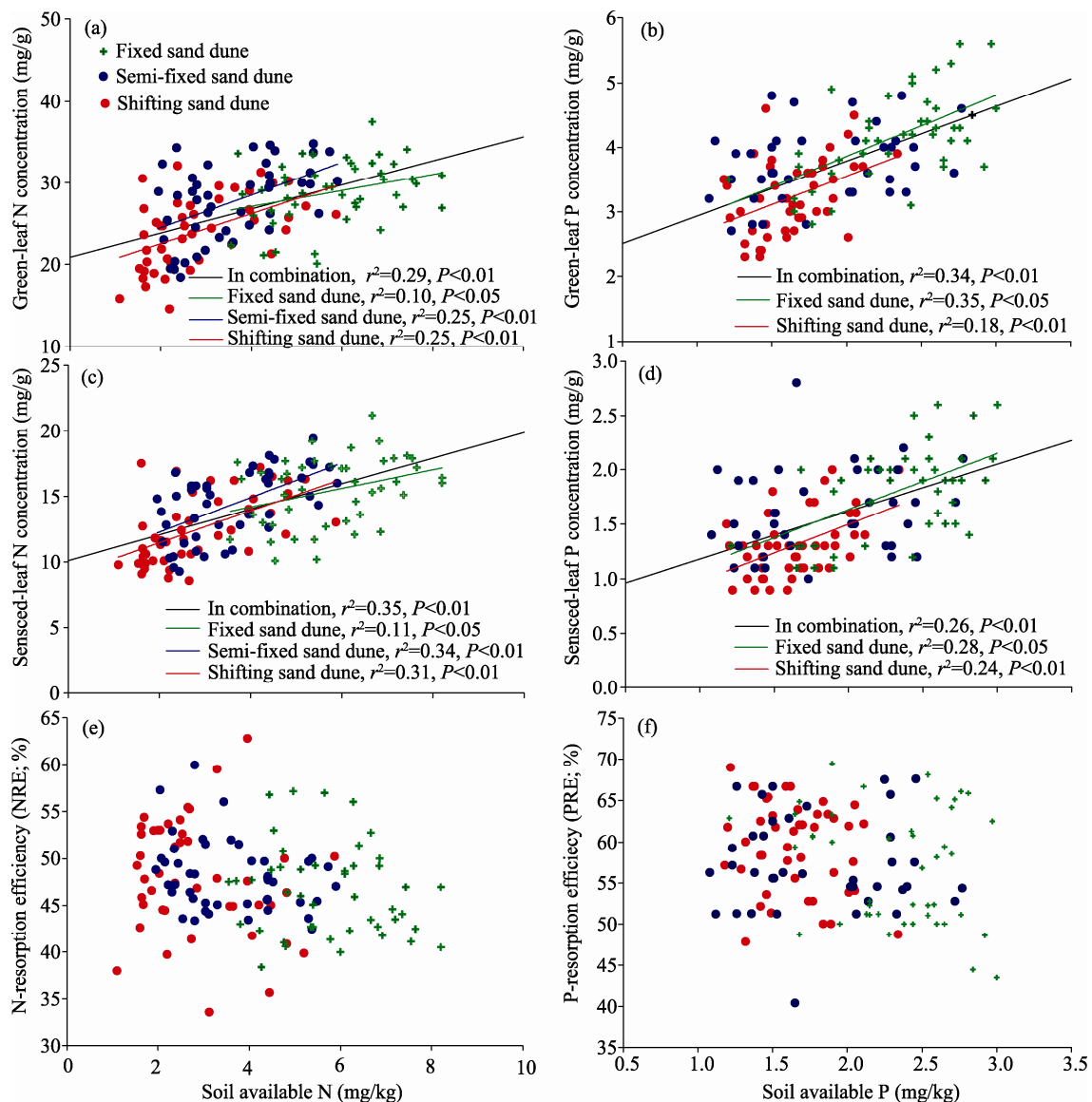


Fig. 3 Relationships between soil available nutrients and foliar nutrient concentrations and resorption efficiencies across three habitats. Only significant regressions are displayed.

A. halodendron across the three habitats (14.1 mg/g) were remarkably higher than that in the senescing leaves of many other deciduous shrubs (12.4 mg/g; Yuan et al., 2005b) and woody species (8.7 mg/g; Killingbeck, 1996). This suggested that *A. halodendron* is unable to reduce N to a low concentration in its senescing leaves. In contrast to N resorption, P resorption was relatively more proficient, with an averaged P concentration (1.6 mg/g) similar to the averaged value of deciduous trees and shrubs (1.6 mg/g; Aerts, 1996) in senesced leaves. In addition, P-resorption proficiency (PRP) in *A. halodendron* was a little lower than that in aster desert shrubs (approximately 2.2 mg/g; Drenovsky et al., 2010) but obviously higher than that in Chenopod desert shrubs (approximately 0.48 mg/g; Drenovsky et al., 2010). Killingbeck (1996), based on data from woody perennials, suggested that any values of nutrient-resorption proficiency in deciduous species less than 7.0 mg/g for N and 0.5 mg/g for P could be considered “complete resorption”, and values greater than 10.0 mg/g for N and 0.8 mg/g for P could be considered “incomplete resorption”. According to these threshold values, both N and P concentrations in senescent leaves of *A. halodendron* show incomplete resorption of N and P in the present study. This implies that pioneer shrub in sand dune environments does not rely heavily on the process of resorption to conserve nutrients.

3.2 Variations in nutrient resorption among different habitats

In spite of the weak selection for N and P conservation, nutrient-resorption proficiencies of pioneer shrub *A. halodendron* varied significantly across the three habitats with distinct nutrient availability. Our study partially supported the hypothesis that higher nutrient-resorption efficiency and proficiency of *A. halodendron* would be observed in infertile habitats such as the shifting sand dune, but lower nutrient-resorption efficiency and proficiency in relatively fertile habitats such as the fixed sand dune. Our results showed that averaged N and P concentrations of *A. halodendron* in senescing leaves across the three sampling years significantly varied from 12.3 and 1.2 mg/g in the shifting sand dune to 15.9 and 1.9 mg/g in

the fixed sand dune, respectively. Similar results were reported by Yuan et al. (2005b) that sandy shrub *Salix gordejewii* growing at shifting sandlands with relatively low fertility had higher NRP than the plants growing at lowlands with relatively high fertility. High NRP in the shifting sand dune in comparison with the fixed sand dune suggests that *A. halodendron* under nutrient limitation is more likely to manage with a low level of nutrients in senescing leaves, giving this species an advantage in infertile soil. In particular, positive relationships between nutrient concentrations in senesced leaves and soil available nutrients indicate that nutrient-resorption proficiencies are more dependent of soil nutrient availability.

However, our study showed that there were no significant differences in both N- and P-resorption efficiencies among the three habitats (Fig. 2) and thus no clear relationships between nutrient-resorption efficiencies and soil available nutrients (Fig. 3), suggesting that N- and P-resorption efficiencies in *A. halodendron* apparently do not explain nutrient conservation strategies over habitats differing in soil fertility. This result is not in accordance with the results by many previous reports that nutrient-resorption efficiency may decrease with increasing soil nutrient availability (Pugnaire and Chapin, 1993; Enoki and Kawaguchi, 1999; Yuan et al., 2005b), but supports the conclusion from Aerts (1996) that there are no clear nutritional controls on nutrient-resorption efficiency.

3.3 Inter-annual variations in nutrient resorption

In rejection of our third hypothesis, foliar N- and P-resorption efficiencies and proficiencies showed little inter-annual variation although annual precipitation varied greatly among the three sampling years. This implies that *A. halodendron* in sand dune environments does not seem to adjust green- and senesced-leaf N and P concentrations in response to significant changes in water availability. This result is not in accordance with some previous reports that inter-annual variation in resorption of N and P by some plant species is statistically significant (Killingbeck, 1993a; Stewart et al., 2008). However, there are still some plant species that do not show changes in re-

sorption of either N or P in response to variation in rainfall (Drenovsky et al., 2010; Renteria and Jaramillo, 2011). These discrepancies may be related to differences in soil texture, which influences soil infiltration rates and water holding capacities. Additionally, the interacting influences of genetics and environments may contribute to the variability of nutrient resorption between years (Stewart et al., 2008). More detailed studies are necessary to understand relationships between rainfall availability, plant morphology, and resorption processes.

Except genetics, soil nutrient availability is considered to be a determinant factor for green- and senesced-leaf N and P resorption (Killingbeck, 1993b). It is, therefore, not surprising that inter-annual resorption of N and P remains steady as limited inter-annual variability was detected in soil available N and P among the three sampling years. Although it is definite that soil water availability is closely related to natural rainfall in arid regions, a water addition experiment in Horqin Sandy Land showed that soil water content was not obviously improved after adding 90 mm of precipitation in growing seasons (Zhang et al., 2008). Since soil net nutrient mineralization rate was positively related to soil moisture (Wang et al., 2006; Giese et al., 2011), especially for soil N, we may speculate that variance of annual rainfall does not influence soil net nutrient mineralization rate in sand dune environments, and thus does not affect foliar nutrient concentration and resorption. Such speculation might be indirectly demonstrated by the above-mentioned water addition experiment in the same ecosystem of Horqin Sandy Land where water addition did not increase grassland productivity which was considered to be more sensitive to soil available nutrients (Zhang et al., 2008). Low soil water holding capacity in loose sand land may be the possible factor that will induce insignificant differences in soil moisture under different rainfall conditions, and thereby result in little difference in soil net nutrient mineralization rate.

3.4 Implications for desertified land restoration in Horqin Sandy Land

Episodes of desertification often result in poor soil

nutrient availability that governs nutrient resorption of plants. However, our results show that pioneer shrub *A. halodendron* in Horqin Sandy Land does not rely more heavily than other plants on the process of resorption to conserve nutrients, which will probably produce significant impacts on the restoration of severely desertified land. Incomplete resorption of foliar nutrients by *A. halodendron*, especially foliar N, contributes to the return of high quality litter to the soil, and thereby indirectly accelerates leaf litter decomposition and nutrient mineralization (Aerts et al., 2007; Lu et al., 2012). Thus, soil nutrient availability in topsoil will be considerably improved, which can potentially create opportunities for the settlement or development of otherwise subordinate or transient plant species (Tewksbury and Lloyd, 2001). This process may accelerate the restoration of desertified land after *A. halodendron* pioneers into shifting sand dunes.

4 Conclusion

In summary, our results suggested that sand-fixing shrub *A. halodendron* would adapt to severely desertified land by nutrient conservation strategies. Firstly, although there were no significant differences in both N- and P-resorption efficiencies in *A. halodendron* among shifting sand dunes, semi-fixed sand dunes and fixed sand dunes, shrubs growing at shifting sand dunes seemed to be more proficient in resorbing nutrient during leaf senescence than those growing at semi-fixed sand dunes and fixed sand dunes. Especially, significant relationships between nutrient-resorption proficiency of individual shrubs and soil available nutrients under shrub canopies indicate that nutrient resorption of *A. halodendron* are more dependent of soil nutrient availability. These traits may facilitate the growth and development of *A. halodendron* in the infertile soil as a pioneer species in Horqin Sandy Land. Secondly, the results showed that there were limited inter-annual variability in foliar N- and P-resorption efficiencies and proficiencies, suggesting that *A. halodendron* in sand dune environments does not seem to adjust green- and senesced-leaf N and P concentrations in response to significant changes in environmental factors. Thirdly, incomplete resorption of nutrients in shrub *A. halo-*

dendron suggests that senesced-leaf fall would return high quality litter to the soil, and thereby would indirectly accelerate litter decomposition and improve soil nutrient availability. The restoration of desertified land, therefore, may be accelerated after *A. halodendron* pioneers into shifting sand dunes.

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