

Plant community C:N:P stoichiometry is mediated by soil nutrients and plant functional groups during grassland desertification

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ABSTRACT

Grassland has sustained serious desertification due to inappropriate human activity in arid and semi-arid areas. This desertification has disrupted ecosystem structure and function. However, desertification on the grassland's C:N:P stoichiometry (Carbon, Nitrogen, and Phosphorus) are poorly understood, which undermines management and restoration of desertified grassland. To improve our knowledge, we studied a desertification gradient in Northeastern China's Horqin Sandy Land to determine the effects of desertification on ecosystem function, the plant community, and soil C:N:P stoichiometry. The soil and plant community C, N and P pools decreased during desertification. Under severe desertification, the soil C:N decreased by 17.4%, versus 39.2% for C:P and 50.1% for N:P. This implies non-proportional losses of soil organic C and nutrients, with the greatest loss for organic C, followed by total N and total P. Plant aboveground C:N and C:P and belowground C:N increased, suggesting increased nutrient utilization efficiency. Canonical correspondence analysis ordination showed that soil N and P significantly affected the plant species composition, which was associated with plant C:N:P. The desertified grassland's fertility (especially N) directly determined the plant community C, N, and P concentrations and C:N:P ratios. The increased dominance of two psammophytes, *Agriophyllum squarrosum* and *Artemisia halodendron* decreased plant community C, N, and P concentrations, but increased C:N and C:P. Thus, plant community C:N:P stoichiometry was mediated by soil nutrients and plant functional groups driven by soil nutrient changes during desertification. The soil nutrient imbalance potentially changed plant community composition, this then altered the soil chemical composition because plant species differ in their element contents and litter inputs. Hence, species with high N content could improve grassland restoration by mitigating N limitations. The native psammophytes *A. squarrosum* and *A. halodendron*, with high stress resistance and resource utilization efficiency, could be applied in desertified grassland restoration.

1. Introduction

Global and regional climate change, combined with increasing human disturbance of ecosystems, has contributed to significant degradation of terrestrial ecosystems, particularly in the form of desertification (Albaladejo et al., 1998; Chen et al., 2014a; Huenneke et al., 2002). Grassland, an important terrestrial ecosystem, has been subjected to continuing overuse and serious desertification, particularly in the arid and semi-arid regions (Dong et al., 2010; Li et al., 2000). This limits the potential for sustainable socioeconomic development, threatens the ecological environment and human health (Kuehn, 2006), and causes widespread decreases in ecosystem productivity,

biodiversity, and soil nutrient contents (Zhao et al., 2009; Zhao et al., 2011; Zhou et al., 2008). Thus, it has changed the cycling of nutrients and other materials. These changes are mediated by the interactions between vegetation and soil (Bui and Henderson, 2013). Therefore, understanding how plant and soil interactions influence the ecosystem's material cycling and elemental balance (stoichiometry) during grassland desertification is crucial to clarify the ecological mechanisms of desertification and provide guidance for management and restoration of desertified grassland.

Abundant evidence indicates that soil organic C, N, and P decrease significantly with increasing desertification (Huang et al., 2007; Xie et al., 2015; Zhao et al., 2009). However, few studies have focused on

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whether the balance among key elements can be maintained during desertification (Jiao et al., 2016; Xie et al., 2015). Delgado-Baquerizo et al. (Delgado-Baquerizo et al., 2013) suggested that decoupling of C, N, and P cycles has occurred in global drylands due to an increase in aridity, which reduces the concentrations of soil C and N but increases that of P in the world's drylands. There are more reasons to expect that desertification could induce an imbalance among soil elements in grassland ecosystems. Desertification may cause a selective loss of soil organic matter and nutrient-rich fine soil particles (Zhao et al., 2009), which results in a disproportional loss of nutrient elements owing to differences in the element ratios of different particle-size fractions (Janzen et al., 1992; Zhao et al., 2009). A recent study along a 3000-km aridity transect in the drylands of northern China demonstrated that soil C:N was positively associated with the sand content but negatively associated with the silt and clay contents, whereas soil C:P and N:P were negatively associated with the sand content but positively associated with the silt and clay contents (Wang et al., 2019). In addition, the aggravation of desertification may also lead to changes in the vegetation community. Previous studies have reported that the vegetation pattern (community structure, species diversity, and plant functional groups) changed as desertification progressed (Huang et al., 2007; Li et al., 2006). Because the biomass chemical composition (nutrient contents and ratios) differs among plant species, changes in community composition could alter the proportions of elements in litter fragments input into soil during desertification (Guiz et al., 2015; Xu et al., 2020; Yuan and Chen, 2015). We hypothesized that the loss of soil nutrient elements that occurs during desertification would not be proportional, and that this difference would modify the balance of soil elements during desertification. This hypothesis can be tested by examining the ratios among elements (i.e., their stoichiometry).

Ecological stoichiometry provides a powerful tool for exploring the effects of desertification on an ecosystem's nutrient balance (Stern and Elser, 2002; Wang et al., 2018). Because the overall stoichiometry of an ecosystem represents the sum of the effects for the component species, community-level stoichiometry provides a strong indication of the ecosystem's elemental balance (Zhang et al., 2018). Several previous studies proposed that plant community C:N:P stoichiometry was affected by the plant community composition, species diversity, and element content of each species (Abbas et al., 2013; Bai et al., 2012), whereas other studies have shown that plant stoichiometry was also shaped by the availability of resources (Bracken et al., 2015; Ordoñez et al., 2009). However, it seems likely that how desertification affects the community-level C:N:P stoichiometry will be complicated, given the complex vegetation–soil feedbacks that occur during the desertification process. Desertification causes species replacement and changes the plant community structure by reducing the availability of growth-limiting resources and the diversity of soil microorganisms (Kerley and Whitford, 2000; Li et al., 2020; Martins et al., 2019; van der Heijden et al., 2008). Changes in plant community structure alter soil resource availability by changing the production and range of organic compounds in the litter fragments that enter the soil, and by changing the composition of microbial communities (Bengtsson et al., 2003; Zak et al., 2003). Thus, the C:N:P stoichiometry of the plant community is influenced by both soil nutrients and the community species composition. Nonetheless, the dominant factors that regulate community C:N:P during desertification remain unclear.

Previous studies mostly focused on the dynamics of plant and soil ecological stoichiometry during succession (Bai et al., 2019; Ma et al., 2020; Su et al., 2019; Yang et al., 2017). However, the mechanisms responsible for these dynamic changes have rarely been investigated, especially in desertified grassland in arid and semi-arid areas. Grassland degradation was accompanied by decreasing concentrations of soil nutrients and changes of the species composition, and these changes might have influenced the ecosystem's elemental balance (Sperry and Hacke, 2002; Xie et al., 2015). Therefore, we designed the present study to explore the mechanisms that control community-level C:N:P during

grassland desertification with the goal of providing guidance for improved management of desertified grassland. We quantified the community-level soil and plant C:N:P stoichiometry and the community species composition in grasslands of different degrees of desertification in the Horqin Sandy Land, northeast China. Specifically, we hypothesized that: (a) The losses of soil organic C, total N, and total P would not be proportional, and as a result, their balance would change during grassland desertification. (b) Plant community C:N:P stoichiometry would be affected by desertification, and this effect would be mediated by changes in the community composition and soil nutrient conditions. To test these hypotheses, we analyzed the relationships among the community C:N:P stoichiometry, soil nutrients, and the functional group composition. Our goal was to reveal which factors had the greatest impact on the community C:N:P stoichiometry during grassland desertification.

2. Materials and methods

2.1. Study area

The study was conducted in the Horqin Sandy Land (118.4°E to 123.5°E, 42.7°N to 45.8°N, at an elevation ranging from 180 to 650 masl), which covers an area of 12.90×10^4 km² in the northeastern part of Inner Mongolia, China. The area has a continental semi-arid to semi-humid monsoon climate. The mean annual temperature ranges from 5.8 °C to 8.3 °C, with mean monthly temperatures varying from −12.6 °C in January to 23.5 °C in August. The mean annual precipitation fluctuates from 300 mm to 500 mm, of which approximately 70% falls from June to August. The mean annual potential evaporation ranges between 1500 and 2500 mm. The mean annual wind velocity ranges from 3.5 to 4.5 m s^{−1}, and the mean wind velocity in spring (the season with the lowest vegetation cover and thus, the greatest vulnerability to erosion) can reach 4.2 to 5.9 m s^{−1}. Windy days with a velocity greater than 17 m s^{−1} occur from 25 to 40 days per year, which results in 10 to 15 days of sandstorms and dust storms, mainly (more than 70% of the total) in the spring.

The Horqin Sandy Land is a sandy dune landscape caused by desertification, with a mosaic distribution of flat or undulating sandy land, mobile dunes, semi-fixed dunes, fixed dunes, and interdune lowlands. The dominant species in the area include annual forbs (*Agriophyllum squarrosum*, *Bassia dasyphylla*, *Artemisia annua*, *Chenopodium acuminatum*, *Artemisia frigida*, *Cynanchum thesioides*), an annual grass (*Setaria viridis*), a sub-shrub (*Artemisia halodendron*), and a shrub (*Periploca sepium*).

The soil in the study area is classified as a Cambic Arenosol (FAO, ISRIC, 1988), in which coarse sand with a particle size of 0.1 to 2.0 mm accounts for 71.1, 77.3%, and 90.0% of the mass at sites with slight, moderate, and severe desertification, respectively, fine sand with a particle size of 0.10 to 0.05 mm, accounts for 19.3, 16.9, and 5.9% of the mass, respectively, and clay and silt, with a particle size <0.05 mm, accounts for 9.6, 5.8, and 4.1% of the mass, respectively (Zhou et al., 2008). The soil organic matter content is 0.08 to 0.49%. The bulk density of soils in areas with slight, moderate and severe desertification was 156.5, 158.1, and 160.2 g cm^{−3}, respectively, with an average (±SE) of 158.0 ± 0.4 g cm^{−3}. The soil pH in the areas with slight, moderate and severe desertification was 7.9, 7.6, and 7.3, respectively, with an average (±SE) of 7.63 ± 0.03 .

2.2. Field sampling

In our study, 75 sampling sites was pseudo-randomly selected (i.e., with approximately equal representation for sites in the three desertification classes), which were distributed from east to west throughout the Horqin Sandy Land (Fig. 1). The sampling sites can be classified into three types: slight desertification (29 sites with a vegetation cover ranging from 31 to 50%), moderate desertification (24 sites with a

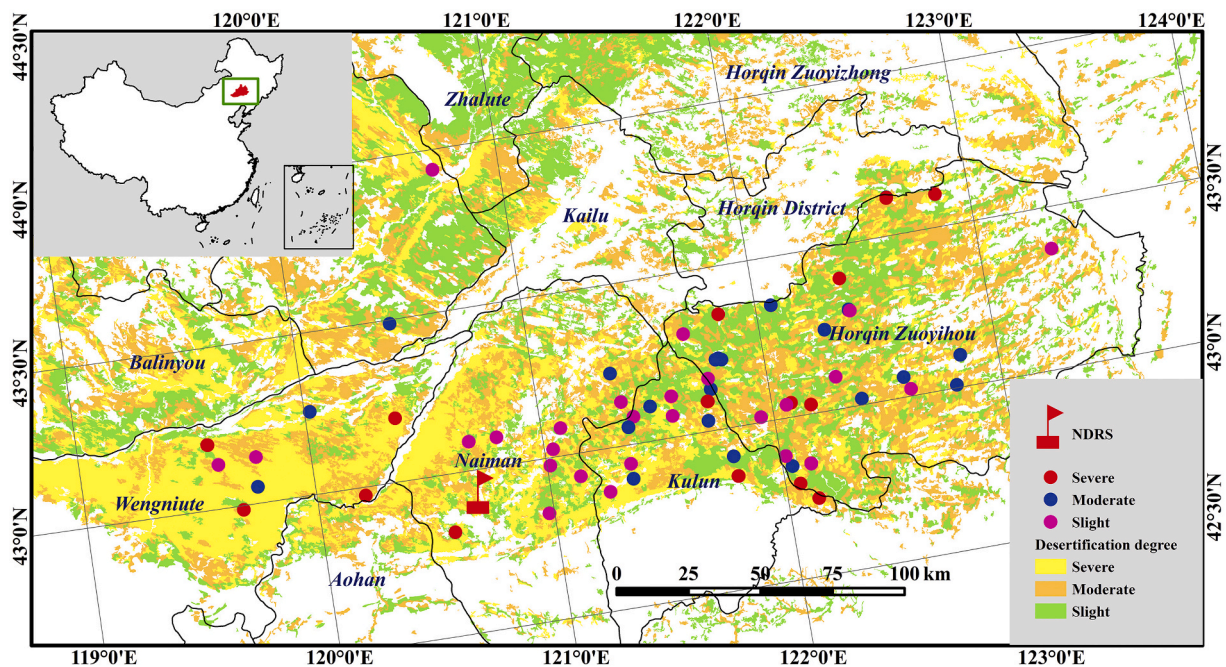


Fig. 1. Distribution of the 75 sample sites in the Horqin Sandy Land. NDRS, Naiman Desertification Research Station.

vegetation cover ranging from 11 to 30%), and severe desertification (22 sites with a vegetation cover less than 10%) with reference to the desertification classification criteria by Zhu and Chen (Zhu and Chen, 1994).

A 100-m transect was established at a random location at each sampling site during the peak of the growing season, and five quadrats (each 1 m × 1 m) at equal 20-m intervals were set along each transect. Within each quadrat, we determined the species composition, and separately harvested all shoots of each species. Three soil cores (8 cm in diameter) were collected in each quadrat to a depth of 100 cm for root sampling. For most samples, roots were washed carefully through a 0.5-mm sieve to remove soil particles, followed by manual removal of large debris and stones. For samples with very fine roots, tweezers were used to handpick fine root from water via a 0.5-mm sieve. Both shoots and roots were oven-dried at 65 °C to constant weight before calculation of the above- and belowground biomass. Within each quadrat, all the shoots were thoroughly mixed into a single composite sample. Then, the roots and shoots were ground and sieved through a 1-mm mesh, separately. Soil samples were randomly collected to a depth of 10 cm at five locations within each quadrat using an auger, and we combined them to create a single composite sample. Soil samples were sieved through a 2-mm mesh to remove roots and other coarse debris. 366 shoot, root, and soil samples were gathered from the sample sites in total. 143 slight, 118 moderate and 105 severe desertification specimens were collected for each type of samples. All samples were ground into a fine powder using a ball mill (GT300 Ball Mill, POWTEQ, Beijing, China) for chemical analysis. Bulk density to a depth of 10 cm in each quadrat was obtained using a cylindrical sampler (5.46 cm in diameter and 10 cm in length).

2.3. Measurement of element concentrations

The C (Carbon) and N (Nitrogen) concentrations of the plant community samples (including both above- and belowground components), the total C and total N concentrations of the soil were measured by an elemental analyzer (ECS4010, Costech, Milan, Italy). Soil inorganic C concentration was measured by a total inorganic carbon analyzer (CM140, UIC, Joliet, IL, USA). Soil organic C concentration was determined by subtracting the total inorganic C concentration from the total C concentration. P concentration of the plant community (above- and

belowground components) was measured by molybdate/stannous chloride method after H₂SO₄-H₂O₂-HF digestion. Soil total P (Phosphorus) concentration was measured by molybdate/ascorbic acid blue method after digestion with HClO₄ and H₂SO₄ (John, 1970). The soil pH was determined from a 1:5 mixture of soil and deionized water using a PHS-3C digital pH meter (MRM Precision Instruments, Brampton, ON, Canada).

2.4. Calculations and data analysis

C, N, and P concentrations of the plant above- and belowground components per unit dry weight were first calculated and then converted to C:N, C:P, and N:P of plant community for later analysis. The C, N, and P pools of soil, as well as above- and belowground biomass were calculated based on the soil bulk density and the corresponding biomass. Species in each quadrat were classified into three functional groups: forbs, grasses, and legumes. Dominance of the functional groups were designated in accord to relative biomass (i.e., proportion of total aboveground community biomass accounted for by each functional group).

One-way ANOVA was adopted for analysis of statistical significance of plant biomass, species diversity, functional group dominance, C, N, and P pools, and stoichiometry of the plant community and soil among the sites with different degrees of desertification. Least Significance Difference (LSD) test was applied to identify statistically significant between pairs of different desertification sites after achieving significant values in ANOVA test. Pearson's correlation coefficient (*r*) was used to quantify the strength of the relationships between pairs of variables. We used general linear models to test for significant relationships between the measured variables. The normality of the variables was evaluated by one-sample Kolmogorov–Smirnov tests. Non-normally distributed data were converted to a normal distribution using a logarithmic transformation. Canonical correspondence analysis (CCA) were used to determine the relative contributions of the soil nutrients to plant species, and association between plant species and community C:N:P. We also used structural equation models implemented with version 3.3.0 of the R software (<https://www.r-project.org/>) to clarify the relationships among the key factors that controlled the stoichiometry. All statistical analyses were performed with version 19.0 of the SPSS software (SPSS,

Chicago, IL, USA). Except for further annotation, statistical significance in this paper was defined as $P < 0.05$.

3. Results

3.1. Plant biomass, species diversity, and plant functional group composition

Both aboveground and belowground biomass and total biomass decreased significantly with increasing grassland desertification (Table 1, $P < 0.001$). Compared with the sites with slight desertification, the above- and belowground biomass and total biomass at sites with moderate desertification site was decreased by 5.52%, 12.05% and 9.92%, and in severe desertification site by 50.33%, 39.44% and 42.99%, respectively. The site with moderate desertification site had the highest species diversity, while the site with severe desertification site showed the lowest species diversity (Table 1, $P < 0.001$). Despite the increase of vegetation degradation (biomass and species diversity decreased) with increasing grassland desertification, the relative proportions of above ground biomass decreased significantly ($P < 0.05$) for grasses and legumes under severe desertification compared to the values for sites with slight and moderate desertification. The relative proportion of forbs increased significantly at sites with severe desertification.

3.2. Soil C, N, and P pools and stoichiometry

Along with the development of desertification, soil C, N, and P pools to a depth of 10 cm showed a significant decrease (Fig. 2, $P < 0.01$). Compared with the values at sites with slight desertification, soil organic C, total N, and total P decreased by 40.0, 25.0, and 9.6%, respectively, at sites with moderate desertification, and by 58.2, 48.5, and 15.6%, respectively, for sites with severe desertification. Total P also slightly varied in moderate to severe desertification sites.

It is noteworthy that the soil C:N, N:P, and C:P ratios also decreased significantly with increasing grassland desertification (Fig. 4, $P < 0.01$), except for no significant difference between the C:N ratios for sites with moderate and severe desertification (Fig. 4, $P > 0.05$). In contrast to the site with slight desertification, C:N, N:P, and C:P decreased significantly by 17.3, 19.0, and 33.9%, respectively, under moderate desertification, and by 17.4, 39.2, and 50.1% under severe desertification.

We found significant positive linear relationships among the soil organic C, total N, total P, and their ratios under slight, moderate, and severe desertification (Fig. 3, $P < 0.01$). These results demonstrate coupled changes of these three soil elements. However, the slopes ($P_a < 0.01$) and intercepts ($P_b < 0.01$) of the linear regression differed significantly among the sites with slight, moderate, and severe desertification ($P < 0.01$), except for the relationship between organic C and total P ($P_a = 0.582$, $P_b = 0.156$) and the intercept for the relationship between total N and total P ($P_b = 0.508$), which suggests that these coupled relationships change with the degree of desertification.

Table 1

Characteristics of the grassland sites as a function of desertification severity. Values are mean \pm SE ($n = 366$).

| Desertification | Biomass | | | Species diversity | | | Community composition (%) | | |
|-----------------|---|---|-------------------------------------|-------------------|------------------|----------------------|---------------------------|-------------------|-------------------|
| | Aboveground biomass (g m^{-2}) | Belowground biomass (g m^{-2}) | Total biomass (g m^{-2}) | Species richness | Simpson Index | Shannon-Wiener Index | Grasses dominance | Legumes dominance | Forbs dominance |
| Slight | 154.77 \pm 4.29a | 319.67 \pm 8.54a | 474.44 \pm 10.66a | 5.32 \pm 0.13a | 0.51 \pm 0.02b | 0.98 \pm 0.03b | 34.27 \pm 2.30a | 13.15 \pm 1.37a | 52.58 \pm 2.43b |
| Moderate | 146.23 \pm 5.28a | 281.14 \pm 5.61b | 427.37 \pm 9.15b | 5.42 \pm 0.16a | 0.57 \pm 0.02a | 1.10 \pm 0.04a | 39.24 \pm 2.88a | 12.03 \pm 1.67a | 48.73 \pm 2.56b |
| Severe | 76.87 \pm 5.73b | 193.60 \pm 10.48c | 270.47 \pm 14.90c | 3.66 \pm 0.17b | 0.46 \pm 0.02b | 0.79 \pm 0.04c | 21.73 \pm 2.01b | 4.86 \pm 1.46b | 73.40 \pm 2.33a |
| <i>F</i> | 67.37 | 57.08 | 81.47 | 38.44 | 9.34 | 16.44 | 12.23 | 8.38 | 26.22 |
| <i>P</i> | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |

Values of a variable followed by different letters differ significantly between degrees of desertification (ANOVA followed by LSD test, $P < 0.05$).

3.3. C, N, and P pools and stoichiometry in the plant community

The C, N, and P pools in plant above- and belowground components decreased significantly with increasing desertification (Fig. 2, $P < 0.01$). As compared to slight desertification, the above- and belowground C pools decreased by 4.6 and 11.7%, respectively, at sites with moderate desertification, and by 50.8 and 38.0% at sites with severe desertification. Compared with slight desertification, the aboveground N pools decreased by 16.2 and 58.3% at sites with moderate and severe desertification, respectively. Belowground N pools decreased by 13.2 and 42.0% at sites with moderate and severe desertification, respectively, in comparison with slight desertification. Compared with slight desertification, the above- and belowground P pools decreased by 25.0 and 17.9%, respectively, at sites with moderate desertification, and by 58.3 and 39.3% at sites with severe desertification.

Desertification had no significant effect on plant belowground N:P and C:P (Fig. 4, $P > 0.05$), but significantly increased the aboveground and belowground C:N and the aboveground N:P and C:P (Fig. 4, $P < 0.05$). In contrast to the sites with slight desertification, the plant above- and belowground C:N increased by 16.7 and 5.4%, respectively, at sites with moderate desertification, and by 16.5 and 10.4%, respectively, at sites with severe desertification. Above ground N:P and C:P increased by 9.5 and 26.5% in moderate desertification and by -1.9 and 13.6% at sites with severe desertification, respectively.

The C and N contents of aboveground components were significantly correlated under moderate desertification, but there was no significant correlation between C and N under slight and severe desertification, and no significant correlations among the contents of the belowground components under slight, moderate, and severe desertification (Fig. A. 1, $P > 0.05$). C and P were significantly negatively correlated in aboveground components under moderate and severe desertification, and for all desertification intensities combined (total) ($P < 0.05$), but there were no significant correlations for the belowground components ($P > 0.05$). N was significantly positively correlated with P in both aboveground and belowground components for all three desertification degrees and for all intensities combined ($P < 0.01$), suggesting that the coupling between community N and P remained strong despite increasing desertification intensity.

We observed many positive correlations ($P < 0.05$, Fig. A. 2) between N contents of plant aboveground and belowground components for all desertification degrees, for P under slight and severe desertification, for C:N under all desertification degrees, and for N:P and C:P under slight desertification and for all intensities combined. These coupled changes hint a proportional distribution of photosynthate and nutrients between the aboveground and belowground components at the community level. The correlations differed somewhat between desertification degrees, probably due to changes in the community composition and soil nutrients during desertification (Table 1).

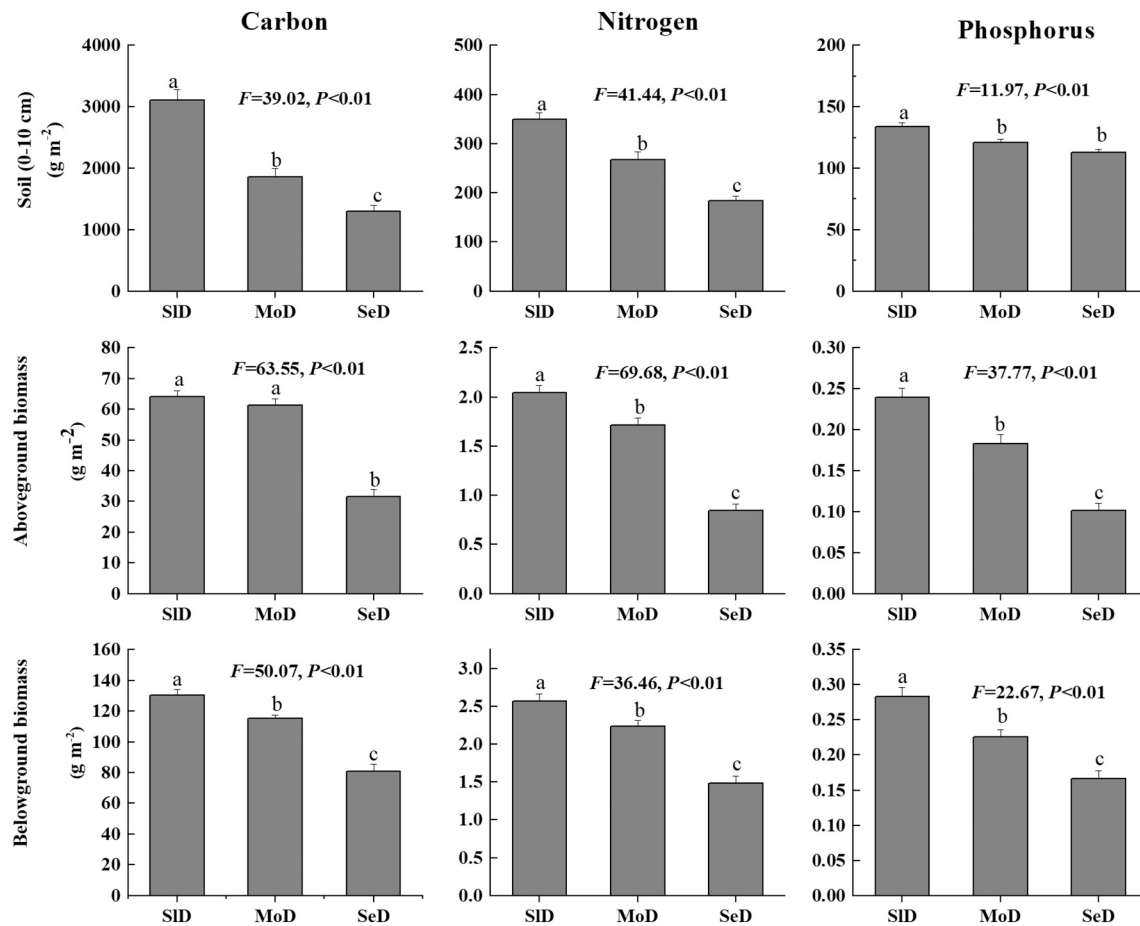


Fig. 2. Effects of desertification on C, N and P pools of soil (0-10 cm) and plant community in Horqin Sandy Land. Desertification level: SID, slight; MoD, moderate; SeD, severe. Values of a variable labeled with different letters differed significantly (ANOVA followed by LSD test, $P < 0.05$, $n = 366$).

3.4. Effect of soil nutrients and plant community composition on community C:N:P stoichiometry

The CCA ordination showed that soil nutrients (soil N and P) were the significant environmental variables affecting plant species composition (Fig. 5, $P < 0.01$). At the sites with low soil nutrient concentrations (the severely desertified grassland), the dominant species were Mr. (*Medicago ruthenica*), As (*Agriophyllum squarrosum*), Pf (*Pennisetum flaccidum*), and Ah (*Artemisia halodendron*). At sites with high soil nutrient concentrations (slightly desertified grassland), the dominant species were Pa (*Phragmites australis*), Aa2 (*Artemisia annua*), Cv (*Chloris virgata*), Ca1 (*Chenopodium acuminatum*), and Cs1 (*Cleistogenes squarrosa*). At the sites with medium soil nutrients (moderately desertified grassland), the dominant species were Sv (*Setaria viridis*) and Cm1 (*Corispermum macrocarpum*). The first CCA axis was strongly correlated with soil N.

The CCA ordination showed that the plant species composition was associated with the plant community C:N:P (Fig. 6, $P < 0.01$). The grasses were associated with higher C:N and C:P, which suggests that the dominant species Pf (*Pennisetum flaccidum*), Ep (*Eragrostis pilosa*) and Aa3 (*Aristida adscensionis*) potentially improved the nutrient utilization efficiency of the community. Legumes with a higher nutrient level and a higher N:P ratio, including the dominant species Al (*Astragalus laxmannii*), Lb (*Lespedeza bicolor*), and Cm2 (*Caragana microphylla*), potentially alleviated N limitation.

To further demonstrate the effects of grassland desertification on plant community C:N:P stoichiometry, main controlling factors (including soil nutrients and community composition) were selected to construct the structural equation models for the aboveground (Fig. 7)

and belowground (Fig. 8) biomass. As shown in the Fig. 7, grassland desertification had a direct negative effect on soil N and P and on species richness. Soil N had direct positive effects on dominance of grasses (0.22, $P < 0.01$) and species richness (0.17, $P < 0.01$), but direct negative effects on dominance of forbs (−0.20, $P < 0.01$). The reduction in soil N caused by desertification decreased community aboveground biomass N and P ($P < 0.05$), and belowground biomass N and N:P ($P < 0.01$, Fig. 8), but increased aboveground biomass C:N and C:P, and belowground biomass C:N ($P < 0.01$). Community aboveground biomass C:N:P ratios were under the direct joint control of soil N and the dominance of grasses and forbs and indirectly regulated by desertification (Fig. 7, $P < 0.05$). The standardized coefficient values representing the effects of soil N were −0.11 for aboveground biomass C, 0.26 for aboveground biomass N, 0.13 for aboveground biomass P, −0.25 for aboveground biomass C:N, and −0.15 for aboveground biomass C:P. These were smaller than the coefficient values for dominance of grasses (−0.13 for aboveground biomass C, −0.61 for aboveground biomass N, −0.24 for aboveground biomass P, 0.45 for aboveground biomass C:N, and 0.26 for aboveground biomass C:P) and dominance of forbs (−0.13 for aboveground biomass C, −0.30 for aboveground biomass N, −0.15 for aboveground biomass P, 0.22 for aboveground biomass C:N, and 0.16 for aboveground biomass C:P). These results implied that the decrease in soil N and altered community composition contribute to changes in community aboveground biomass C:N:P during grassland desertification.

Structural equation model for depicting the effects of grassland desertification on community belowground biomass C:N:P also included soil nutrients and community composition (Fig. 8). Community belowground biomass C:N:P was directly regulated by the combined effects of

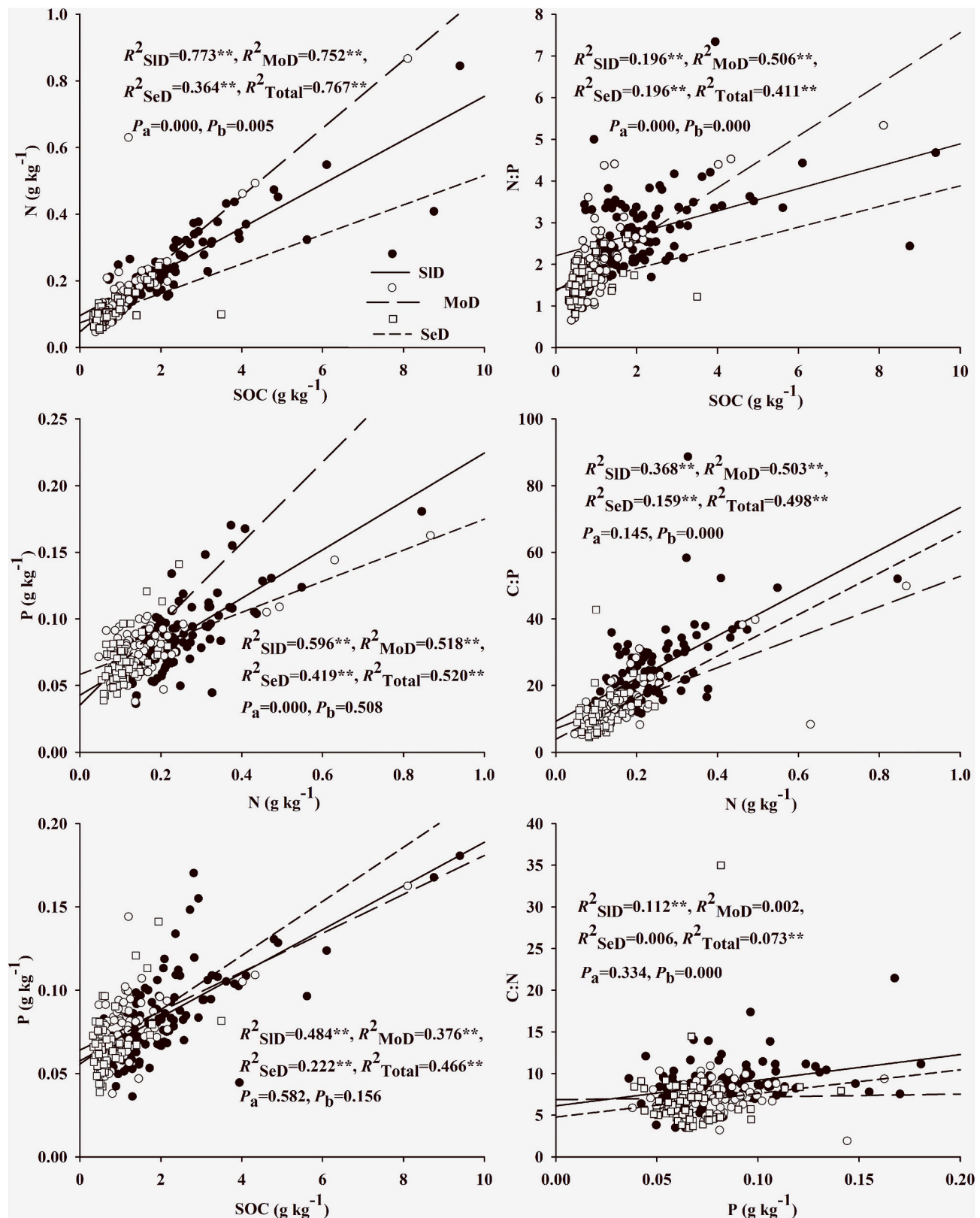


Fig. 3. Relationships (general linear model R^2 values) between soil organic C (SOC), total N, and total P concentrations, and stoichiometry. Desertification levels: SID, slight; MoD, moderate; SeD, severe; total, all three severities combined. Significance ($n = 366$): * $P < 0.05$ and ** $P < 0.01$ for the regressions; $P_a < 0.05$ for the slope and $P_b < 0.05$ for the intercept for significant differences between the desertification levels.

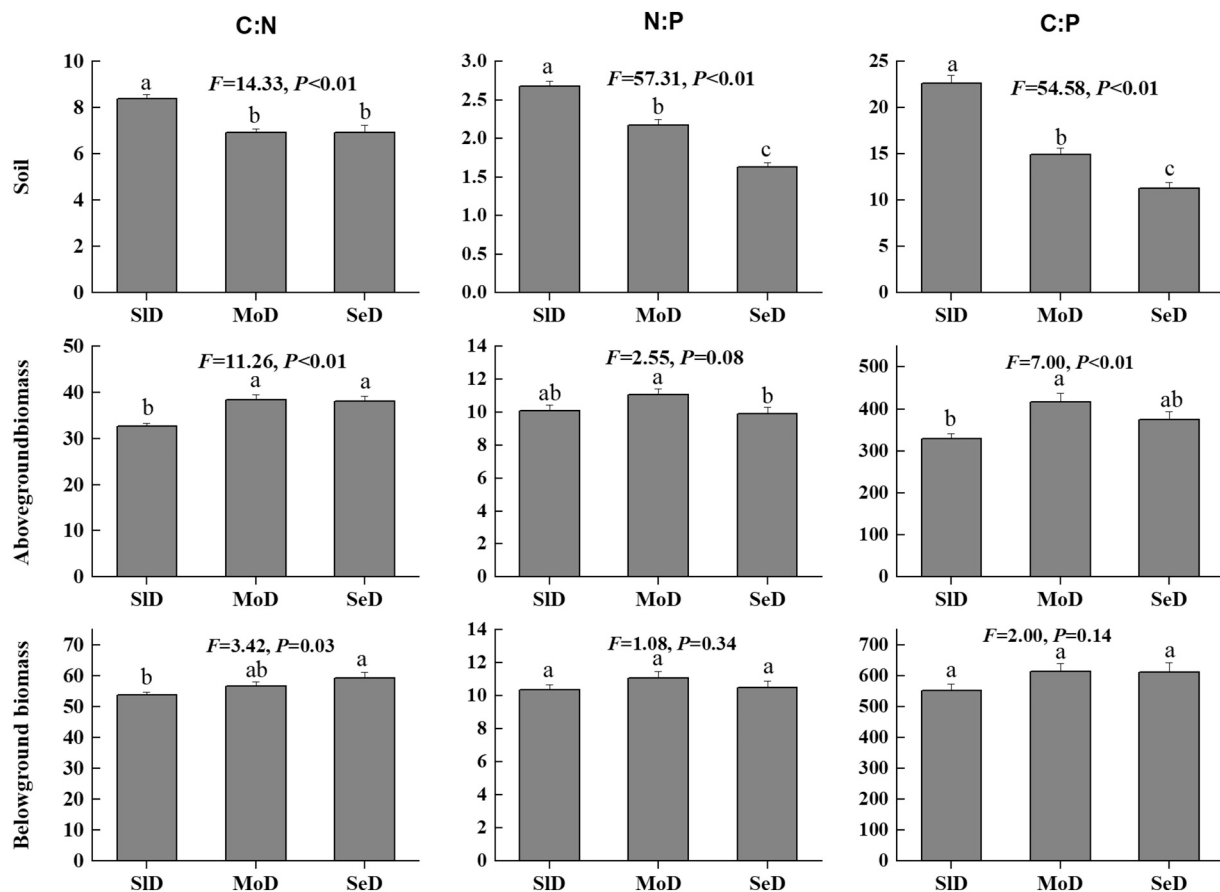


Fig. 4. Effects of desertification on the C:N:P stoichiometry of the soil (0–10 cm) and plant in Horqin Sandy Land. Desertification level: SID, slight; MoD, moderate; SeD, severe. Values of a variable labeled with different letters differed significantly (ANOVA followed by LSD test, $P < 0.05$, $n = 366$).

soil N, species richness, and dominance of grasses, and indirectly regulated by desertification and soil P (Fig. 8, $P < 0.05$). The standardized coefficient values representing direct effects of soil N and species richness on belowground biomass N (both 0.31), belowground biomass C:N (−0.30 and −0.29, respectively), and belowground biomass N:P (0.19 and 0.20, respectively) were higher than those for the dominance of grasses (−0.14 for belowground biomass N, 0.17 for belowground biomass C:N, and 0.17 for belowground biomass N:P).

4. Discussion

4.1. Nutrient imbalances that result from grassland desertification

Our results indicate that soil C, N, and P pools decreased dramatically with increasing grassland desertification. This is most likely a direct consequence of substantial reductions in soil organic C, total N, and total P contents, rather than due to changes of soil bulk density (Table A. 1). Aeolian desertification can seriously damage soil nutrients by causing a selective loss of organic matter and nutrient-rich fine soil particles (Hennessy et al., 1986; Zhao et al., 2006; Zhou et al., 2008). The resulting reduction of soil productivity decreases inputs from litter and dead roots to the soil, which further reduces soil nutrients. The effect of desertification on plant C, N, and P pools in this study were consistent with previous studies (Gao et al., 2015). Grassland desertification reduced C, N, and P pools in community above- and belowground biomass, mainly due to decreases in above- and belowground biomass rather than relatively minor changes in the C, N, and P contents of above- and belowground biomass (Table A. 2). The essential nutrients for plant growth are mainly acquired from mineralization of organic material, which depends on the activity of soil microbes. However,

inputs of shoots and dead roots to the soil decreased, and the microbial population was also likely to change due to the altered soil conditions (e.g. a decrease in soil C:N and species diversity) during grassland desertification (Bengtsson et al., 2003; Xie et al., 2015). Reduction of microbial degradation of organic matter would lower soil productivity. In summary, grassland ecosystem functions (the plant community and soil C:N:P pools, soil productivity) were undermined during grassland desertification via vegetation-soil feedbacks.

Although soil organic C, total N, and total P decreased significantly with increasing desertification, their C:N, C:P, and N:P ratios also decreased dramatically, implying that the losses of soil organic C, total N, and total P were not proportional, and that the decreases occurred in the following order: organic C > total N > total P. The higher proportion of soil organic C loss than that of total N can be attributed to the fact that light-fraction materials and clay and silt particles with a high C:N ratio can be easily removed by wind erosion (Chen et al., 2014a; Janzen et al., 1992; Zhao et al., 2009). In addition, decreases in litter and root inputs from shoots and dead roots could explain why organic C and total N, which depend on mineralization of organic matter, were lost faster than total P, which depends on weathering of the parent material (Zhang et al., 2017). Indeed, our correlation analysis indicated that the coupling relationships among soil organic C, total N, and total P were altered during grassland desertification, which suggests that the balance among the elements varied as desertification continued. Similar results were obtained by Jiao et al. (Jiao et al., 2016), who reported a soil C-N-P decoupling event in a similar site in Inner Mongolia, China. They observed a decrease in soil C:P and N:P ratios and an increase in the soil C:N ratio with increasing aridity and temperature along a 3500-km transect through a temperate climate zone. The response of nutrient losses to desertification differs among ecosystem types. For instance, the

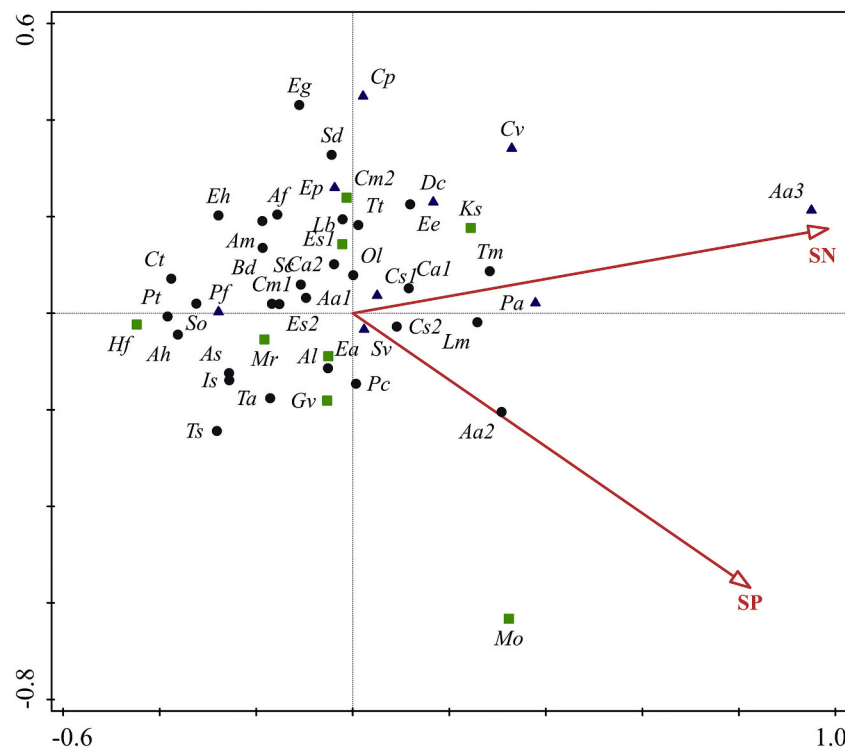


Fig. 5. Canonical correspondence analysis ordination showing the effect of soil nutrients on the plant species. SN, soil N, $P = 0.002$; SP, soil P, $P = 0.002$. $R^2 = 0.32$. Species abbreviations are shown in the appendix (Table A. 3). Green squares, legumes; blue triangles, grasses; black circles, forbs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rate of P decreased was greater than the rate of N decrease during ecosystem degradation in an alpine meadow (Wen et al., 2013), whereas soil nutrient loss in a desert grassland was ranked in the order $N > C > P$ (Wu et al., 2018). These different patterns of nutrient element loss might be associated with the different causes of degradation (e.g., soil erosion, grazing, freezing and thawing), which influence the cycling of mineral nutrients to different extents (Delang, 2018).

Our study showed that desertification also altered plant community C:N:P stoichiometry. Structural equation modeling (Figs. 7, 8) indicated that the reduction of soil nutrients led directly to the decreases of community aboveground biomass N and P, and belowground biomass N and N:P. This means that the grassland desertification exacerbated nutrient limitations. With decreasing soil N as a result of grassland desertification, the community-level aboveground biomass C:N and C:P, and the belowground biomass C:N increased. These increases suggest that the desert plant community can maintain a high utilization efficiency for soil nutrients under resource-limited conditions as a result of the community's plasticity and ability to adapt to its harsh environment (Aerts and Chapin, 1999; Berendse and Aerts, 1987). With ongoing desertification, the N:P of aboveground biomass decreased slightly, and fall below the previously established N:P threshold of 14 to 16 that defines the threshold between N and P limitation (Güsewell and Verhoeven, 2006; Koerselman and Meuleman, 1996). This probably indicated that desertification reinforces N limitation potentially. Despite the minor loss of soil P with increasing desertification, the increasingly serious desertification would increase the potential of grassland to experience future N and P co-limitation. In our study, the C:N:P stoichiometry of belowground biomass (except for a slight increase in C:N) was not greatly affected by desertification. A study of a grassland ecosystem in Inner Mongolia, China, reported dramatic effects of grazing on the C, N, and P contents of belowground biomass, but the C:N:P stoichiometry remained unexpectedly resilient (Bai et al., 2012). Thus, it is possible that the community-level belowground C:N:P stoichiometry in our desertified grassland ecosystem can adapt to external

disturbances, which might be a survival strategy of plants in resource-poor settings such as our grasslands.

4.2. Community C:N:P stoichiometry was influenced strongly by the plant functional group composition during grassland desertification

The increasingly severe desertification caused a decrease in soil nutrients and a shift in community composition (Table 1, Table A. 1). However, research has shown that the changes in community composition are closely related to changes in soil nutrient conditions during grassland desertification (Xie et al., 2015). Tilman (Tilman, 1982, 1987) proposed that the composition of the plant community is shaped by the availability of water, nutrients, and other resources. In addition, the change in species diversity is closely related to soil nutrient gradients (Bai et al., 2010). During grassland desertification, changes in the plant community composition might have resulted from the increasing spatial and temporal variations in soil resources (Sperry and Hacke, 2002). Indeed, we observed a decrease in the soil organic C, total N, and total P contents, accompanied by a decrease of species richness and diversity under severe desertification, as well as changes in the composition of the plant functional groups. (Table 1, Table A. 1). The CCA ordination showed that soil nutrients (N and P) were associated with species changes (Fig. 5). For example, the dominant species Mr. (*M. ruthenica*), As (*A. squarrosus*), Pf (*P. flaccidum*), and Ah (*A. halodendron*) were found at sites with low soil nutrient contents, whereas the dominant species Pa (*P. australis*), Aa2 (*A. annua*), Cv (*C. virgata*), Ca1 (*C. acuminatum*), and Cs1 (*C. squarrosa*) were found at sites with high soil nutrient contents, and the dominant species Sv (*S. viridis*) and Cm1 (*C. macrocarpum*) were distributed in sites with medium soil nutrient contents. Combined with field survey data, we observed that the most obvious changes were in two psammophytes, As (*A. squarrosus*) and Ah (*A. halodendron*), which share a high resource-utilization efficiency and were mainly distributed in moderate and severe desertified grassland.

As a pioneer annual psammophyte adapted to mobile sand dunes in

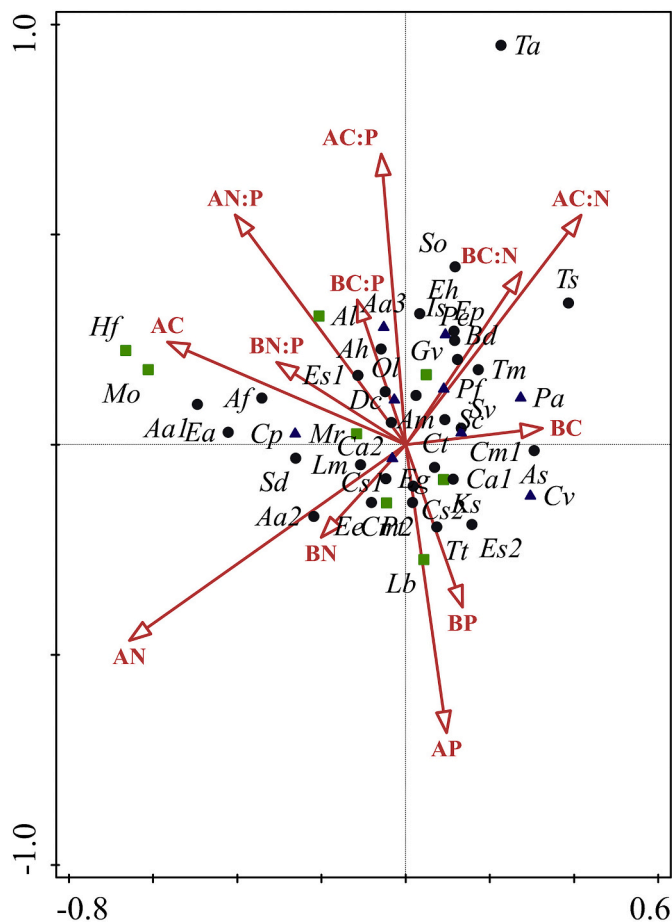


Fig. 6. Canonical correspondence analysis ordination showing the relationships between the plant species and community biomass C:N:P stoichiometry (ratios). AC/BC, aboveground/belowground biomass C; AN/BN, aboveground/belowground biomass N; AP/BP, aboveground/belowground biomass P; AC/N/BC/N, aboveground/belowground biomass C:N ratio; AN/P/BN/P, aboveground/belowground biomass N:P ratio; AC/P/BC/P, aboveground/belowground biomass C:P ratio. $R^2 = 0.20$. Species abbreviations and significance are shown in the appendix (Table A. 3 and Table A. 5). Green squares, legumes; blue triangles, grasses; black circles, forbs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

arid and semi-arid regions of Central Asia, *As* (*A. squarrosus*) has a range of physiological, morphological, and ecological adaptations that let it colonize unstable, nutrient-poor, and drought-prone, and hot sand dunes (Liu et al., 2006). Because its seeds can be used as a food crop with high nutritional value (Chen et al., 2014b), it may be a good choice for stabilizing and restoring severely desertified grassland. *Ah* (*A. halodendron*) is one of the dominant native sand-fixing shrub species that is found on semi-mobile and semi-fixed dunes and that is well adapted to windy and sandy environments; as a result, the species is widely used in vegetation restoration in our study area (Su et al., 2005). In our study, *A. squarrosus* and *A. halodendron* accounted for 34 and 23% of the forbs, respectively, in the severely desertified grassland, respectively, and *A. halodendron* accounted for 40% of forbs in moderate desertified grassland. Due to colonization by these two sand-fixing plant species during grassland desertification, we observed a decrease in the dominance of grasses, and an increase in the dominance of forbs. Previous studies showed that grasses prefer a conservative resource-use strategy, characterized by high leaf and root C:N and C:P ratio (Ning et al., 2017).

The CCA ordination also showed that the grasses were associated with higher community biomass C:N and C:P (Fig. 6). In contrast, forbs,

with high N and P contents and a high capacity for nutrient uptake and utilization, need high levels of soil nutrients to maintain their growth. Thus, the grasses, with their conservative resource-use strategies, should (in theory) have a competitive advantage over the forbs in the infertile soil that develops during grassland desertification (Suding et al., 2005). However, the strong adaptability of *As* (*A. squarrosus*) and *Ah* (*A. halodendron*) in the resource-poor desertified environment resulted in higher dominance by forbs than by grasses during grassland desertification. The dominance of legumes did not change significantly during the early stages of desertification, but decreased markedly and significantly in the later stages of desertification. This suggested that legumes could not survive on mobile dunes with scarce nutrients, despite their ability to capture additional N through biological N fixation in desertified grassland with a N limitation (Guo et al., 2017). But the legumes were more frequently used for vegetation improvement after sand fixation. It will be necessary to carry out in-depth research to determine whether they survive well enough to make this a good choice.

Previous studies reported that changes in the availability of soil nutrients (Su et al., 2006), community composition (Zuo et al., 2009), and microbial communities (Dhillon and Zak, 1993) were important mechanisms that were responsible for desertification-induced changes in plant community C:N:P stoichiometry. In the present study, community C:N:P stoichiometry appears to have been mediated by these factors (Figs. 7, 8), and mainly influenced by changes in the functional group composition driven by changes in soil nutrient conditions. Structural equation modeling showed that the decrease in soil nutrients and the altered community composition that resulted from this decrease resulted in changes in community biomass C:N:P. On one hand, the site fertility directly determined the aboveground and belowground community-level C:N:P. Decreased soil N led to decreased community N and P, and to increases of community C:N and C:P, which represent adaptive response to a growing nutrient limitation in stressed habitats. On the other hand, changes in the plant assemblage would alter community-level element composition because species and plant functional groups differ in their element uptake and concentrations (Guiz et al., 2015). Increased aboveground biomass C:N and C:P was mainly due to increasing proportions of the two psammophytes with higher C:N and C:P *A. squarrosus* and *A. halodendron*, which replaced grasses and legumes.

Interestingly, the species richness was associated with the community-level belowground biomass C:N:P. We observed that with decreasing species richness during grassland desertification, belowground biomass N and N:P both decreased, but C:N increased (Fig. 8). Previous studies have reported a linkage between trends in the plant community (species richness and diversity, functional group composition) and trends in the community C:N:P (Abbas et al., 2013; Guiz et al., 2015). Ptacnik et al. (Ptacnik et al., 2010) suggested that with increasing diversity, terrestrial plants can increase their nutrient more efficiently than their C fixation. We theorized that plants in a less diverse community and a resource-poor environment must invest more in rigid root structure to compete more effectively for nutrients and water. This requires an increase in the C concentration relative to the N concentration, resulting in an observable increase in the belowground biomass C:N ratio. Therefore, desertification altered the community composition in response to soil nutrient conditions, and this affected the community-level C:N:P stoichiometry. This stoichiometry would reflect adjustments by the plant species to adapt to local conditions and species replacement during grassland desertification.

In summary, the imbalance of soil nutrients that develops during desertification could induce changes in the plant community composition, which, in turn, could alter the chemical composition of the soil through changes in the litter supplied to the soil because plant species differ in their nutrient contents. This feedback would aggravate the imbalance of soil nutrient elements that develops during grassland desertification. Our results suggest that the desertified grassland is suffered from N limitation, which further might be exacerbated result from

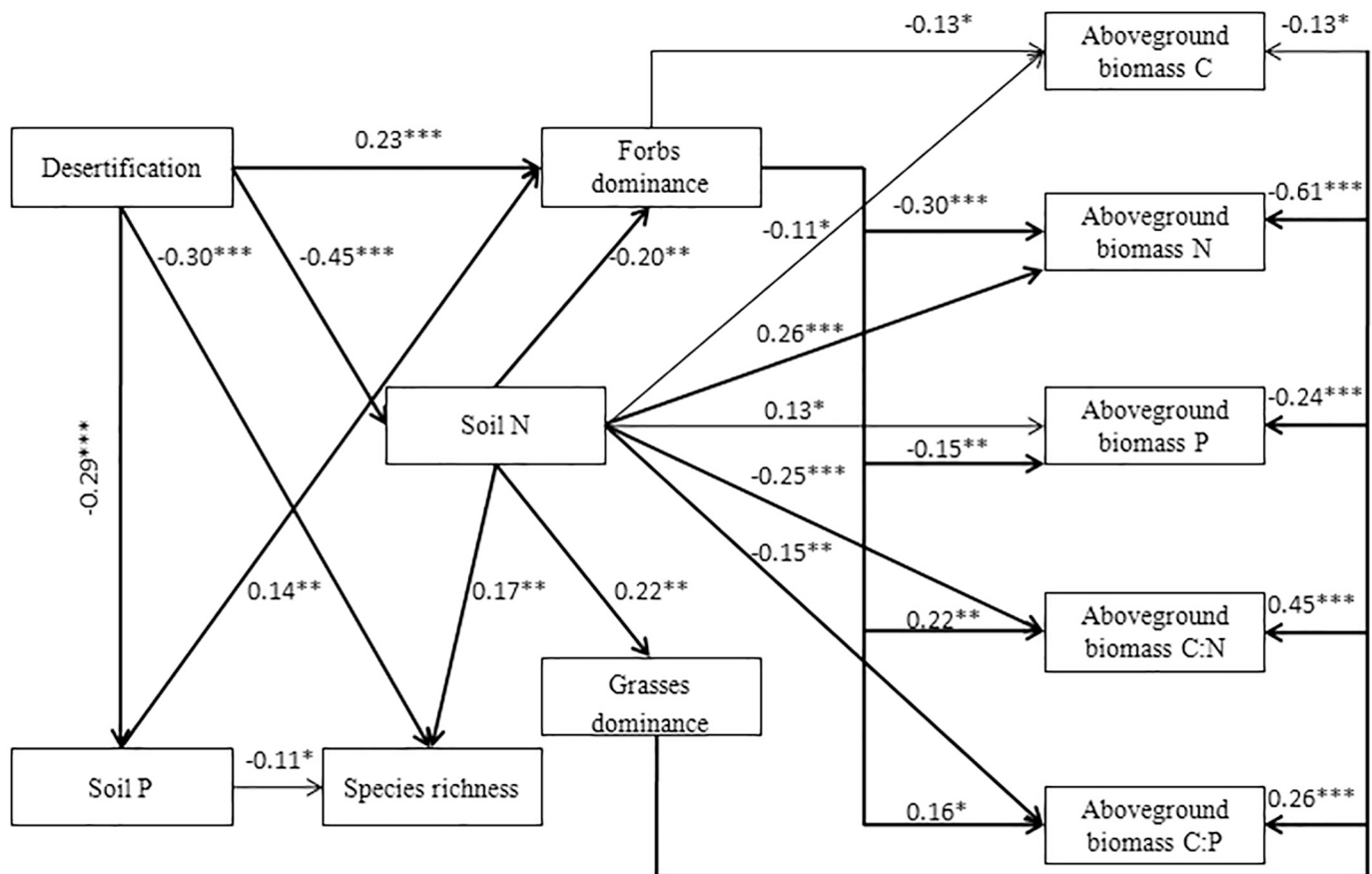


Fig. 7. Structural equation modeling depicting the effect paths of grassland desertification, soil nutrients, and community species composition on aboveground biomass C, N, and P concentrations, and the associated ratios (C:N:P). Numbers on the paths represent the standardized regression weights. Significance: *, **, and *** represent significance of the paths at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

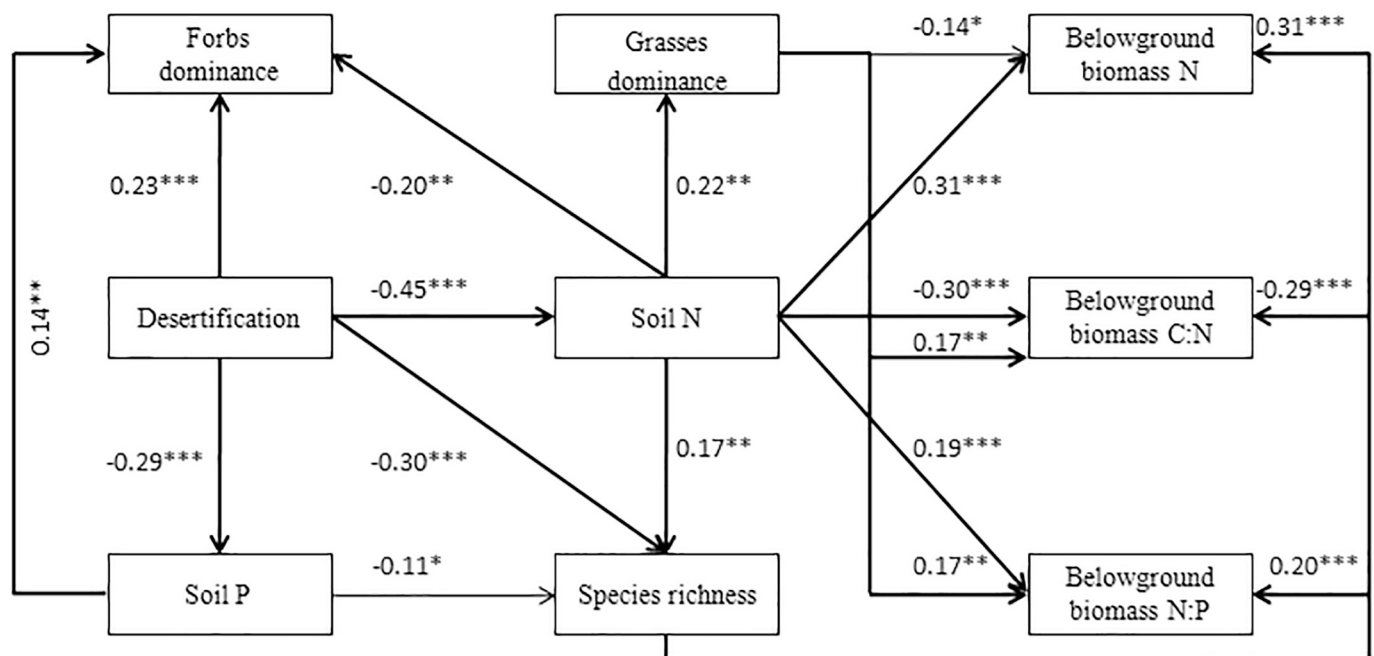


Fig. 8. Structural equation modeling depicting the effect paths of grassland desertification, soil nutrients, and community species composition on belowground biomass C, N, and P concentrations, and the associated ratios (C:N:P). Numbers on path is the standardized regression weights. Significance: *, **, and *** represent significance of the paths at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

the development of desertification. Therefore, plant species with a high N content could potentially be used to relieve the N limitation in this area. However, a large area of artificial poplar (*Populus simonii*) forest was established during the 1970s to combat desertification and control dust storms in the Horqin Sandy Land (Wang et al., 2010). Poplars, which have a low leaf N content, might not be suitable for balancing nutrient elements in a desertified grassland (Chomel et al., 2015). Consequently, nitrogen-fixing species and forbs with high N contents should be planted to fix sand dunes, and relieve N limitation in the soil. However, as we noted earlier, the suitability of legumes for desertified grassland sites must be confirmed through future research. This will be essential to improve the management and restoration of the desertified grassland. In addition, the native psammophytes *A. squarrosus* and *A. halodendron*, with high stress resistance and resource-utilization efficiency, could be applied in artificial sand-fixing vegetation in desertified grassland to control desertification and improve the regional environment.

Author contributions

Yulin Li conceived and designed the study based on discussions involving Zhiying Ning, Jie Lian, Hongling Yang, and Yuqiang Li. Zhiying Ning, Xueyong Zhao, Lilong Wang, and Yulin Li performed the experiments. Zhiying Ning and Lilong Wang analyzed the results. Zhiying Ning drafted the manuscript. All co-authors had a chance to review the manuscript before submission and contributed to discussion and interpretation of the data.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2021.106179>.

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