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# Changes in species diversity, aboveground biomass, and vegetation cover along an afforestation successional gradient in a semiarid desert steppe of China

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ABSTRACT

Afforestation is a key technique for the control of desertification and environmental deterioration in arid and semiarid regions. Therefore, it is important to quantify the influence of the succession that results from afforestation on biodiversity conservation and ecological environment. Here, we describe a case study in the sand-binding vegetation communities in China's semiarid desert steppe in which we evaluated the effects of afforestation and key ecological processes on the community characteristics, and explored the ecological mechanism of the succession paradigm of afforestation in arid and semiarid regions. 42 species from 20 families and 40 genera along the afforestation successional gradient were collected during a comprehensive vegetation survey in 2013. The community was dominated by species in the Leguminosae, followed by the Poaceae, Compositae, and Zygophyllaceae. Our results show that the succession significantly affected community and habitat characteristics. The numbers of families, genera, and species decreased primarily during succession and then increased sharply to a maximum. Species diversity appeared to reach its maximum towards the middle of the succession, and shrubs had a greater contribution and accounted for 80.6% of the community biomass, whereas herbaceous plants contributed 64.8% of the total vegetation cover. Soil crusts significantly altered the rainfall infiltration and redistributed soil water balance, and water in the 40- to 100-cm soil layer played a decisive role in vegetation productivity and cover. Therefore, the interactional feedback between vegetation development, soil crusts and soil water was the main driver responsible for the feedback mechanism of the succession paradigm for the sand-binding vegetation communities in the semiarid desert steppe of China.



## 1. Introduction

The desert steppe is a critical component of China's grassland ecosystem (Kang et al., 2007), and covers 34.7% of China's northern grasslands (Zhang et al., 2014). It thus plays important roles in China's ecological environment, biodiversity conservation, and socioeconomic characteristics at a regional scale (Kang et al., 2007; Wang and Ba, 2008). However, human activities have led to declining biodiversity and vegetation cover, along with accelerated soil erosion (Zhou et al., 2002; Alrababah et al., 2007). Consequentially, desertification has become one of the most serious environmental problems in China during the last half century, and threatens the survival and sustainable development of human at both local and regional scales (Jiang et al., 2006). Therefore, afforestation has been used as the major ecological project to control desertification and environmental deterioration with the sand-binding vegetation by restoring the vegetation cover in China, and provides a paradigm of successful desertification mitigation in the world's desert regions (Houerou, 2000; Chen and Duan, 2009; Li et al., 2009).

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Afforestation affects natural resources and biodiversity conservation during the restoration of forested landscapes because it is expected to promote secondary succession in desert steppe ecosystems (Huebner and Vankat, 2003; Baessler and Klotz, 2006; Amici et al., 2012; Souza et al., 2013). In addition, vegetation restoration can be viewed as a continuous process from establishment of the new vegetation to successful development of attributes that seem likely to improve ecosystem resilience and stability in both the short term and the long term (Alrababah et al., 2007; Zhu et al., 2009; Yang et al., 2012). Therefore, afforestation has gained increasing attention in desert steppe ecosystems (Alhamad, 2006; Alrababah and Alhamad, 2006). However, biodiversity changes during the different stages of the succession that follows afforestation (Jing et al., 2014), which has recently generated great debate over several conflicting hypotheses about this change (Howard and Lee, 2003). One hypothesis is that biodiversity should increase continuously as succession continues, since the ecosystem complexity increases (Vallauri et al., 2002; Ruiz-Jaén and Aide, 2005; Rayfield et al., 2005; Letcher and Chazdon, 2009; McClain et al., 2011; Sansevero et al., 2011). A second hypothesis suggests that biodiversity is greatest at the beginning of succession and gradually decreases as a result of processes that affect succession (Chapin et al., 2002; Gárdenfors, 2001; Souza et al., 2013). A third hypothesis predicts that biodiversity will increase from early succession to reach a maximum at mid-succession, followed by a decrease during late succession (Aubert et al., 2003; Malacska et al., 2004; El-Sheikh, 2005; Zhu et al., 2009; Suganuma et al., 2014). A fourth hypothesis predicts that there will be no general pattern for changes in biodiversity during forest succession (Zhu et al., 2009; Bu et al., 2014). Therefore, effective conservation of biodiversity in the face of increasing human impacts and ongoing environmental change will require a better understanding of the influence of afforestation on the species composition, community structure, and biodiversity of ecosystems at both regional and global scales.

Desert steppes are among the ecosystems that are most vulnerable to environmental changes associated with human disturbance in China (Jing et al., 2014). The species richness is lower than that in humid regions (Coppedge et al., 2008), so that the fragile ecological environment makes biodiversity conservation even more important (McNeely, 2003; Liu et al., 2009) because species loss is more significant in desert steppes than the equivalent loss in a species-rich ecosystem (Al-Eisawi, 2003; McNeely, 2003; Liu et al., 2009). Biodiversity conservation can help to improve the sustainability of a desert steppe's natural resources with the sand-binding vegetation by controlling desertification. However, afforestation can also decrease biodiversity (Brockerhoff et al., 2008; Bremer and Farley, 2010), with widespread species loss and the replacement of endemic and specialist species by ruderal and exotic species (Bremer and Farley, 2010; Souza et al., 2013). More importantly, afforestation can increase desiccation of soils and have negative effects on the long-term sustainability of forest ecosystems in regions such as the Loess Plateau of China (van Dijk and Keenan, 2007; Jiao et al., 2012). Therefore, the effects of afforestation on the species composition and biodiversity of ecosystems has been debated around the world.

In China, little work has been done to determine the effects of afforestation processes on biodiversity conservation in semiarid desert steppes. In this paper, we presented a study on the influence of afforestation on the species composition, aboveground biomass, and vegetation cover of the sand-binding vegetation communities in semiarid desert steppes of China to determine whether key ecosystem processes have been restored and whether the restored system will be ecologically sustainable, with a high potential for biodiversity conservation. Our specific objectives were (1) to describe the species composition, aboveground biomass, and vegetation cover along a chronosequence of post-afforestation succession; (2) to examine the influence of the interaction between afforestation and environmental variables on the characteristics of community succession; (3) to determine the ecological mechanism of the succession paradigm for the artificial sand-fixation plant community; and (4) to evaluate whether the restoration accomplished by afforestation has been ecologically successful. The results will improve our understanding of the mechanisms that underlie ecosystem stability during the succession caused by afforestation in the semiarid desert steppes of China.

## 2. Materials and methods

### 2.1. Study area

The study area is located in an ecotone between prairie and desert steppe, in Yanchi County of the Ningxia Hui Autonomous Region in China, between 37°40′N and 38°10′N and between 106°30′E and 107°41′E (Fig. 1). The region has a semiarid continental monsoonal climate characteristic of the mid-temperate zone. Annual temperature averages 8.1 °C, and ranges from a minimum monthly mean of −24.2 °C in January to a maximum of 34.9 °C in July. Annual precipitation ranges from 250 to 350 mm, with a mean of 289.4 mm, and about 62% of the total rainfall falls

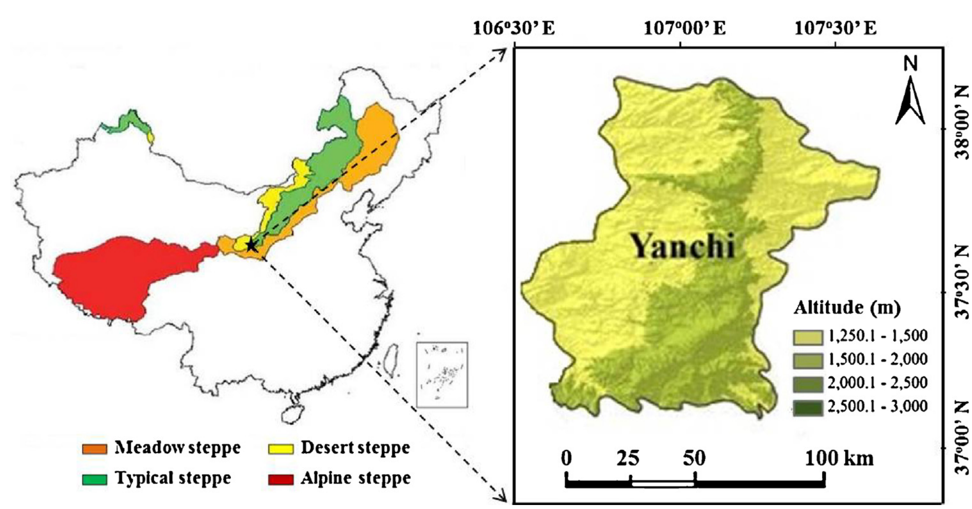


**Fig. 1.** (Left) Distribution of the four main steppe types in China. Source: Kang et al. (2007). (Right) Map of the study area.

between July and September. There is abundant sunshine (an annual average of 3124 h) and high potential evaporation (an annual average of 2897 mm). The growing season is from May to October, and the frost-free period lasts about 165 days, with long winters. Gales occurs an average of 23.4 times per year, with a wind speed of more than 8 m $s^{-1}$, and sand or dust storms occurs an average of 20.6 days per year. These conditions contribute to frequent sandstorm disasters and exacerbate the sandy desertification that is occurring in China.

The region is a typical transitional zone between the Maowusu Sandy Land in the northeast to the Loess Plateau in the south. From north to south, the climate changes from arid to semiarid and the vegetation type changes from desert steppe to steppe vegetation. This geographic transition is accompanied by changes in the species diversity, natural resources, and vulnerability of the ecological environment. The zonal soil changes from an eolian sandy soil (a sierozem) in the north to a dark loessial soil (a chernozem) in the south, with some saline soils, planosols, and other soil types. The vegetation types are dominated by shrub communities, grasslands, meadows, and sandy or desert vegetation. Shrubs (e.g., *Salix psammophila* and *Caragana microphylla*) account for a high percentage of the vegetation cover and are widely distributed. The arid grassland is dominated by *Stipa grandis*,*Stipa bungeana*, *Agropyron cristatum*, and *Thymus serpyllum* var. *mongolicus*. The desert steppe is dominated by *Caragana tibetica*, *Oxytropis aciphylla*, *Nitraria sibirica*, and *Kalidium foliatum*.

### 2.2. Measurements

We selected the sand-binding vegetation communities that had undergone succession for 3, 8, 13, 18, 23, 28, 33, and 43 years after afforestation with *Caragana korshinskii*. At each site, we conducted a comprehensive investigation of the vegetation types. Plantation age was determined from data provided by the Forestry Bureau of Yanchi County in China, supplemented by interviews with managers of local forestry stations. The vegetation survey used a nested sampling design and was conducted from August to October 2013. We used five 200 m × 200 m plots for each duration after afforestation. There were differences between topography, soil type and spatial heterogeneity (patches) for each plantation age. The plots had no natural forest vegetation, and were dominated by shrubs and herbs. We established five 10 m × 10 m shrub subplots within each overall plot and 10 quadrats (1 m × 1 m) for herbaceous vegetation in each subplot. All samples were obtained far from the edges of the plot to avoid edge effects. In each subplot and quadrat, we determined the numbers of each plant species, and measured its height, crown area, coverage, and aboveground biomass of all shrubs and herbaceous species. We also measured the basal diameter, the average branch length, and the number of branches for all shrubs. Vegetation cover was determined using the crown-projection method, and the abundance and number of individuals were recorded using coenological and statistical methods. Aboveground biomass was measured in each subplot and sampling quadrat; for herbs, we directly sampled the aboveground biomass in every sampling quadrat and weighted with 0.01 g of electronic weighing scales. The individual shrubs were cut down at ground level, and the total weight was obtained in the field using a hanging scale (accuracy = 0.1 kg), and fresh subsamples of wood and twigs with leaves were collected from five individuals per species. All samples including herbs and shrubs stored in sealed plastic bags, and transported to the laboratory where fresh and oven-dried weights (air-forced oven at 80 °C) were obtained to estimate the water content (percent) per species. We calculated the aboveground biomass of shrubs using a multispecies above ground dry biomass regression models developed by Conti and Díaz (2013) and Conti et al. (2013). To classify the species, we followed the botanical nomenclature of the Institute of Botany, Academia Sinica (IBAS, 1983) and the Flora Reipublicae Popularis Sinicae from the Flora of China (www.efloras.org). The plant functional group was based on the definitions of Bai et al. (2004): annual and perennial herbs, shrubs, and sub-shrubs.

During the survey period, we also investigated the environmental characteristics of the subplots: the soil type, soil bulk density, soil moisture content, soil crust thickness, and a community stability index (CSI). We determined CSI using the following scores: for mobile dunes, CSI = 0; for semi-mobile dunes with vegetation cover less than 10%, CSI increases from 0 to 1 with increasing vegetation cover; for semi-mobile and semi-fixed dunes with vegetation cover between 10 and 30%, CSI increases from 1 to 2 with increasing vegetation cover; for semi-fixed dunes with vegetation cover from 30 to 50%, CSI increases from 2 to 3 with increasing vegetation cover; for fixed dunes, with vegetation cover from 50 to 70%, CSI increases from 3 to 4 with increasing vegetation cover; and for fixed dunes with vegetation cover greater than 70%, CSI increases from 4 to 5 with increasing vegetation cover. Soil moisture was measured in each plot, subplot, and quadrat in 2013 at 10-day intervals throughout the year of 2013, the measurements were obtained by means of oven-drying, at 20-cm intervals from 0 cm to a depth of 200 cm, with three replicates in every layer. Soil type and bulk density were measured at the same locations as soil moisture. The position of each plot and subplot was determined using a GPS receiver (eTrex Vista Cx, Garmin, http://www.garmin.com). We also recorded the elevation, slope, slope aspect (including "no direction" for flat ground, or E, S, W, N, NE, SE, SW, and NW, recorded as a categorical variable with values ranging from 0 to 8, respectively), and soil crust thickness. We collected data for a total of 8 plantation ages using 40 plots

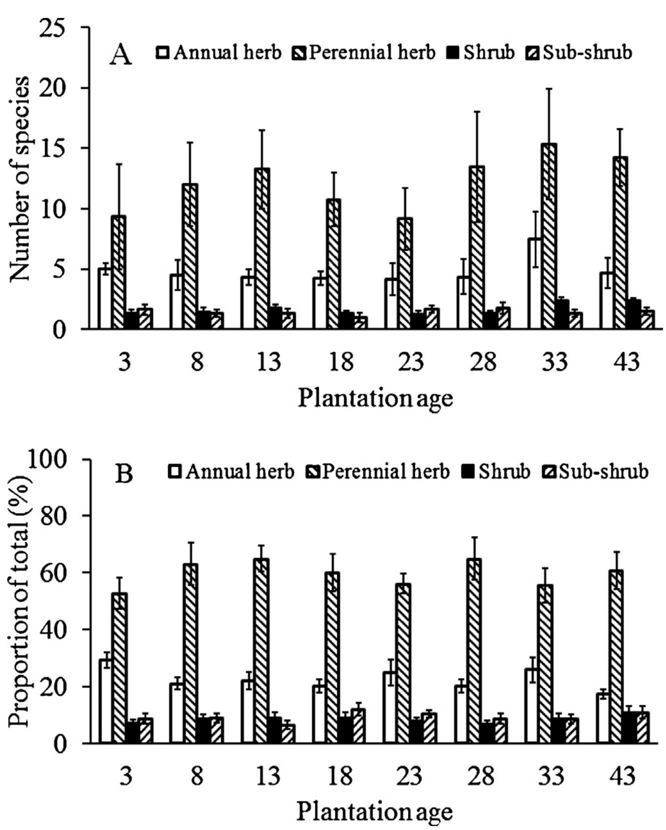


**Fig. 2.** Patterns and dynamics of the plant life-form composition as a function of plantation age in a semiarid desert steppe of China. Values are means ± SEM for a parameter.

**Table 1**
Patterns and dynamics of the numbers of plant families, genera, and species with increasing plantation age in a semiarid desert steppe of China.[a]

| Plantation age (years) | No. of families | No. of genera | No. of species | Leguminosae | | Poaceae | | Compositae | | Zygophyllaceae | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Species | Proportion of total (%) | Species | Proportion of total (%) | Species | Proportion of total (%) | Species | Proportion of total (%) |
| 3 | 12.12 ± 0.32ab | 23.10 ± 2.34a | 19 ± 1.44bc | 7.12 ± 1.34a | 30.43 ± 5.65a | 3.21 ± 0.34a | 13.04 ± 1.67c | 2.21 ± 0.45cd | 8.70 ± 2.21cd | 1.32 ± 0.43a | 4.35 ± 0.76a |
| 8 | 10.23 ± 1.20bc | 17.05 ± 2.43b | 17 ± 1.35c | 5.14 ± 0.67ab | 29.41 ± 4.34ab | 3.45 ± 0.54a | 17.65 ± 2.65abc | 4.34 ± 0.54abc | 23.53 ± 3.43ab | 2.34 ± 0.45a | 11.76 ± 1.43a |
| 13 | 9.05 ± 2.24c | 13.67 ± 1.34d | 20 ± 1.54bc | 4.43 ± 0.64bc | 20.00 ± 2.43bcd | 5.23 ± 0.56a | 25.00 ± 3.45ab | 3.32 ± 0.45bcd | 15.00 ± 2.47bcd | 3.32 ± 0.32a | 15.00 ± 2.32a |
| 18 | 8.78 ± 1.43c | 14.14 ± 2.54cd | 15 ± 0.78c | 2.45 ± 0.87c | 13.33 ± 1.98d | 4.21 ± 0.45a | 26.67 ± 4.56a | 1.14 ± 0.43d | 6.25 ± 0.94d | 2.21 ± 0.43a | 13.33 ± 1.67a |
| 23 | 8.15 ± 1.23d | 12.23 ± 1.67d | 16 ± 1.98c | 3.35 ± 0.34bc | 18.75 ± 2.23bcd | 4.35 ± 0.65a | 25.00 ± 3.45ab | 1.21 ± 0.32d | 6.67 ± 0.87d | 1.32 ± 0.67a | 6.25 ± 0.98a |
| 28 | 9.24 ± 2.23c | 17.04 ± 2.87b | 20 ± 1.40bc | 5.23 ± 0.56ab | 25.00 ± 3.45abc | 3.56 ± 0.67a | 15.00 ± 2.43bc | 6.43 ± 0.87a | 30.00 ± 2.65a | 2.24 ± 0.65a | 10.00 ± 1.45a |
| 33 | 13.27 ± 2.52a | 23.67 ± 3.65a | 27 ± 1.98a | 3.12 ± 0.43bc | 17.65 ± 3.32cd | 3.67 ± 0.98a | 17.05 ± 2.32abc | 5.56 ± 0.67ab | 29.41 ± 3.32a | 2.21 ± 0.76a | 11.76 ± 2.87a |
| 43 | 10.22 ± 1.56bc | 16.34 ± 2.54bc | 23 ± 1.86ab | 3.24 ± 0.23bc | 13.04 ± 1.23d | 3.65 ± 1.20a | 13.04 ± 1.87c | 4.32 ± 0.65abc | 17.39 ± 2.43bc | 1.23 ± 0.32a | 4.35 ± 0.76a |
| Mean value | 9.88 ± 0.64 | 16.88 ± 1.48 | 18.88 ± 1.09 | 4.00 ± 0.57 | 20.95 ± 2.37 | 3.50 ± 0.27 | 19.13 ± 1.99 | 3.25 ± 0.65 | 17.12 ± 3.44 | 1.75 ± 0.25 | 9.60 ± 1.46 |

[a] Means for a parameter followed by different letters differ significantly (Tukey's HSD, $P < 0.05$).

(200 m × 200 m), 200 subplots (10 m × 10 m), and 2000 quadrats (1 m × 1 m) nested within the plots and subplots.

### 2.3. Data analysis

#### 2.3.1. Species diversity

Species diversity was characterized using α-diversity and β-diversity, and was represent with species richness (S, the number of species) and Sørensen index for the shrub and herb strata within each subplot and quadrat, respectively. The importance value (IV, %) for the plant species was calculated using the following formula (Zhang et al., 2005):

$$IV = \frac{RD + RC + RF}{3} \quad (1)$$

where *RD* is the relative density (the ratio of the number of individuals of a species to the total number of individuals of all species, %); *RC* is the relative cover (the ratio of the cover of a species to the total cover of all species, %), and *RF* is the relative frequency (the ratio of the percentage frequency of a species to the total frequency of all species, %) (Jiang et al., 2007).

$$\text{Sørensenindex}: \beta_{cs} = \frac{2c}{(a+b)} \quad (2)$$

where *a* and *b* represent the number of species in two samples, and *c* is the number of species shared by the two samples.

#### 2.3.2. Statistical analysis

To assess how the community characteristics changed along a chronosequence of afforestation, we performed one-way ANOVA and Tukey's HSD test (after testing for homogeneity of variance and confirming a normal distribution) and considered values to be significantly different at $P < 0.05$. All statistical analysis was performed using version 13.0 of the SPSS software (SPSS Inc., Chicago, IL, USA). We analyzed the effects of the environmental variables on community succession using repeated-measures ANOVA to compare the main effects and the interactive effects among plantation age, soil bulk density, soil moisture, soil crust thickness, and the number species, community biomass, and vegetation cover. When values differed significantly at $P < 0.05$ in the ANOVA, we used post hoc least-significant-difference (LSD) tests to identify which values differed significantly. We also used constrained ordination to test for relationships among the parameters that we analyzed. This technique is analogous to multivariate multiple regression and was chosen because it performs well with nonorthogonal data and data with a collinear gradient (McGarigal et al., 2000; Robertson et al., 2009). We used redundancy analysis (RDA) to explore the influence of the environmental characteristics (plantation age, longitude, latitude, elevation, slope, aspect, CSI, soil crust thickness, soil moisture, soil bulk density, soil type) on the community species composition, aboveground biomass (community biomass, shrub biomass, herb biomass), and vegetation cover (community cover, shrub cover, herb cover). This analysis was performed by using version 4.5 of the Canoco software (University of South Bohemia, Ceske Budejovice, Czech Republic).

## 3. Results

### 3.1. Changes in floristic composition and life forms during succession

We collected a total of 42 species from 20 families and 40 genera, with 37 herbaceous species and 5 shrub and sub-shrub species. The numbers of families, genera, and species decreased slowly during succession, reaching their minimum value in year 23, and then increased sharply to a maximum in year 33 (Table 1). The average community composition, all plantation ages combined, was 9.9 families, 16.9 genera, and 18.9 species. The succession process significantly affected the community composition for families ($F_{2,7} = 5.81$, $P < 0.01$), genera ($F_{2,7} = 32.20$, $P < 0.001$), and species ($F_{2,7} = 16.98$, $P < 0.001$) along the afforestation succession sequence for the *Caragana korshinskii* community (Table 1). Over the entire range of ages, the community was dominated by species in the Leguminosae (21.0% of the total), followed by the Poaceae (19.1%), Compositae (17.1%), and Zygophyllaceae (9.6%). The differences in the number of species among the plantation ages were significant for the Leguminosae ($F_{2,7} = 4.57$, $P < 0.01$) and the Compositae ($F_{2,7} = 5.91$, $P < 0.01$), but not for the Poaceae and Zygophyllaceae (Table 1). Moreover, the changes in species number was not consistent with the changes in the number of families along the succession sequence, and they showed different patterns (Table 1).

The community succession significantly affected the number of species ($F_{2,7} = 12.78$, $P < 0.001$) and the proportion ($F_{2,7} = 7.63$, $P < 0.001$) of annual herbs, but not significant for perennial herb, shrub and subshrub (Fig. 2). Herbs dominated the composition of the understorey vegetation, and the species numbers changed for the hyperbolic with two vertices, whereas the species numbers were significantly higher for all four life forms in year 33 than during the rest of the sequence (Fig. 2). The corresponding proportions of the total species number, averaged across all plantation ages, were 59.6 ± 1.6% for perennial herbs, 22.7 ± 1.4% for annual herbs, 9.4 ± 0.6% for sub-shrubs, and 8.4 ± 0.4% for shrubs. However, sub-shrubs had the greatest change for the proportion (CV = 18.6%), followed by annual herbs (17.0%), perennial herbs (7.6%), and shrubs (14.6%) across all plantation ages.

We grouped plants into four life forms, and there were four dominant herbaceous species based on the community importance value (*Salsola pellucida*, *Radix polygalae*, *Setaria viridis*, and *Corispermum tylocarpum*) and two dominant shrub species (*Caragana korshinskii* and *Cynanchum komarovii*). With the succession of plant communities, the predominant species had transferred from one age to another in herbaceous community, but the differences were not statistically significant in the shrub community because of the simple community structure, which had few species with high dominance. In contrast, the dominant species significantly changed in the herbaceous community across

**Table 2**
The dynamics of the importance values (*IV*) for the 42 species as a function of plantation age in a semiarid desert steppe of China.

| Number | Species | *IV* as a function of plantation age (years) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 3 | 8 | 13 | 18 | 23 | 28 | 33 | 43 |
| Herbs (annual and perennial) | | | | | | | | | |
| 1 | *Salsola pellucida* | 15.29 | 7.17 | 42.76 | 14.74 | 12.77 | 16.42 | 5.91 | 35.94 |
| 2 | *Radix polygalae* | 2.40 | 1.79 | 2.35 | 10.00 | 5.27 | 1.18 | 2.77 | 1.36 |
| 3 | *Setaria viridis* | 5.62 | 40.19 | 0.94 | 13.46 | 9.79 | 4.35 | 26.12 | 20.44 |
| 4 | *Corispermum tylocarpum* | 12.28 | 1.18 | 0.92 | 19.83 | 33.49 | 7.94 | 7.84 | 3.15 |
| 5 | *Cleistogenes squarrosa* | 0 | 0.74 | 1.30 | 2.44 | 0 | 6.67 | 2.50 | 6.59 |
| 6 | *Peganum harmala* | 0.72 | 1.23 | 25.00 | 1.09 | 0 | 0 | 0 | 1.53 |
| 7 | *Agropyron cristatum* | 5.59 | 0 | 3.10 | 2.18 | 5.91 | 2.18 | 0 | 0 |
| 8 | *Sophora alopecuroides* | 0 | 3.11 | 0 | 2.02 | 2.59 | 2.76 | 0 | 3.97 |
| 9 | *Heteropappus hispidus* | 0.73 | 1.95 | 0 | 0 | 0 | 4.06 | 6.04 | 1.45 |
| 10 | *Artemisia frigida* | 0 | 6.14 | 0 | 2.37 | 3.13 | 0.71 | 0 | 1.53 |
| 11 | *Euphorbia kozlovii* | 2.35 | 1.20 | 0 | 0 | 1.50 | 0.71 | 0 | 6.72 |
| 12 | *Oxytropis aciphylla* | 0 | 0 | 7.35 | 1.89 | 20.14 | 0 | 0 | 4.71 |
| 13 | *Limonium sinense* | 1.42 | 1.38 | 0 | 8.09 | 5.38 | 0 | 8.30 | 1.65 |
| 14 | *Thermopsis lanceolata* | 0 | 2.46 | 0 | 0 | 0 | 0.95 | 12.90 | 1.28 |
| 15 | *Cuscuta chinensis* | 0 | 0.56 | 0 | 2.69 | 1.24 | 0 | 0 | 3.26 |
| 16 | *Eragrostis pilosa* | 0 | 0.57 | 0 | 2.57 | 1.28 | 0 | 1.23 | 0 |
| 17 | *Pennisetum centrasiaticum* | 40.65 | 0 | 0 | 12.06 | 17.66 | 0 | 0 | 0 |
| 18 | *Plantago asiatica* | 8.80 | 0 | 0 | 0 | 0 | 0 | 4.00 | 14.55 |
| 19 | *Stipa capillata* | 0 | 0 | 6.59 | 0 | 0 | 0 | 11.22 | 2.52 |
| 20 | *Ixeris chinensis* | 1.82 | 9.63 | 0 | 0 | 0 | 3.58 | 0 | 0 |
| 21 | *Tribulus terrestris* | 0 | 1.20 | 0 | 1.32 | 0 | 0.79 | 0 | 0 |
| 22 | *Oxytropis bicolor* | 0 | 0 | 0 | 2.09 | 0 | 0 | 0 | 17.01 |
| 23 | *Oxytropis psammocharis* | 0.73 | 0 | 5.21 | 0 | 0 | 0 | 0 | 0 |
| 24 | *Agriophyllum squarrosum* | 1.59 | 3.76 | 0 | 0 | 0 | 0 | 0 | 0 |
| 25 | *Echinops gmelini* | 0 | 0 | 0 | 1.16 | 0 | 0 | 4.02 | 0 |
| 26 | *Sagittaria sagittifolia* | 0 | 0 | 2.95 | 0 | 0 | 0 | 0 | 1.32 |
| 27 | *Melilotus suaveolens* | 0 | 0 | 0 | 0 | 0 | 40.85 | 0 | 0 |
| 28 | *Linum usitatissimum* | 0 | 13.45 | 0 | 0 | 0 | 0 | 0 | 0 |
| 29 | *Clerodendrum fortunatum* | 0 | 0 | 0 | 0 | 0 | 0 | 5.70 | 0 |
| 30 | *Hedysarum scoparium* | 0 | 0 | 0 | 0 | 0 | 0 | 4.68 | 0 |
| 31 | *Inula salsoloides* | 0 | 0 | 0 | 0 | 0 | 2.85 | 0 | 0 |
| 32 | *Dodartia orientalis* | 0 | 0 | 0 | 0 | 0 | 0 | 2.54 | 0 |
| 33 | *Bassia dasyphylla* | 0 | 1.11 | 0 | 0 | 0 | 0 | 0 | 0 |
| 34 | *Serratula chinensis* | 0 | 0 | 0.98 | 0 | 0 | 0 | 0 | 0 |
| 35 | *Artemisia annua* | 0 | 0 | 0 | 0 | 0 | 0.71 | 0 | 0 |
| 36 | *Scorzonera divaricata* | 0 | 0.58 | 0 | 0 | 0 | 0 | 0 | 0 |
| 37 | *Herba taraxaci* | 0 | 0.58 | 0 | 0 | 0 | 0 | 0 | 0 |
| Shrubs and sub-shrubs[a] | | | | | | | | | |
| 1 | *Caragana korshinskii* (S) | 40.17 | 72.24 | 59.90 | 54.74 | 78.96 | 49.60 | 23.53 | 60.61 |
| 2 | *Hedysarum scoparium* (S) | 0 | 0 | 0 | 0 | 0 | 0 | 4.68 | 0 |
| 3 | *Cynanchum komarovii* (sub-S) | 59.83 | 27.76 | 40.10 | 20.64 | 21.04 | 10.27 | 3.00 | 15.39 |
| 4 | *Hedysarum laeve* (sub-S) | 0 | 0 | 0 | 0 | 0 | 30.49 | 13.13 | 15.90 |
| 5 | *Artemisia ordosica* (sub-S) | 0 | 0 | 0 | 4.47 | 0 | 9.64 | 55.27 | 8.00 |

[a] S, shrub; sub-S, sub-shrub.

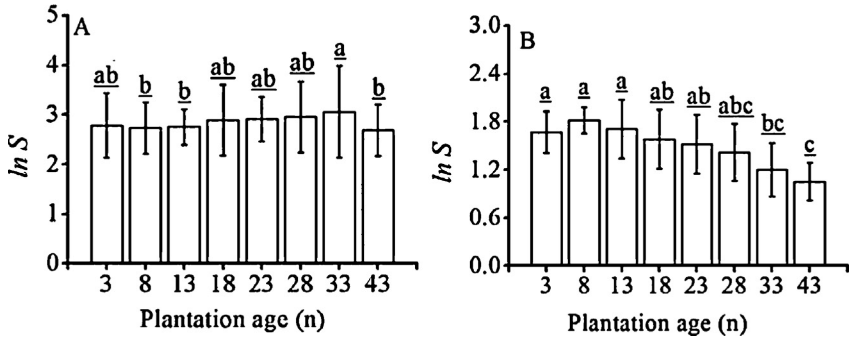


**Fig. 3.** The changes in the species richness (ln *S*) of (A) herbaceous species (annual and perennial) and (B) shrub species (shrubs and sub-shrubs) as a result of succession in a semiarid desert steppe of China. Means followed by different letters differ significantly (Tukey's HSD, $P < 0.05$).

all plantation ages, e.g *Pennisetum centrasiaticum*, *Setaria viridis*, *Salsola pellucida*, *Corispermum tylocarpum*, *Melilotus suaveolens*, *Setaria viridis* and *Salsola pellucida* (Table 2). However, for most of the rare species that occurred only once across all plantation ages, which the importance values was less than 5, e.g *Melilotus suaveolens*, *Linum usitatissimum*, *Clerodendrum fortunatum*, *Hedysarum scoparium*, *Inula salsoloides*, *Dodartia orientalis*, *Bassia dasyphylla*, *Serratula chinensis*, *Artemisia annua*, *Scorzonera divaricata*, and *Herba taraxaci*, but besides *Melilotus suaveolens* and *Linum usitatissimum*.

### 3.2. Changes in species diversity during succession

The diversity of species was significantly affected by succession for the herbaceous ($F_{2,7} = 2.64$, $P < 0.05$) and shrub species richness ($F_{2,7} = 3.99$, $P < 0.01$) (Fig. 3). The diversity of herbaceous species increased gradually during succession, and up to the maximum value for the herbaceous in year 33, while shrub species in year 8 and then down to the minimum value in year 43 (Fig. 3). Overall, species diversity is very low with fewer species and small variation in semiarid desert steppe of China.

The change of Sørensen index showed a bimodal curve during succession, and the species turnover increased with the increase of plantation age, and up to the maximum value between year 8 and year 13. While, the similarity of species composition between succession arrived the maximum value from 18 to 23 year, which means that the species change lied in the most stable stage (Fig. 4).

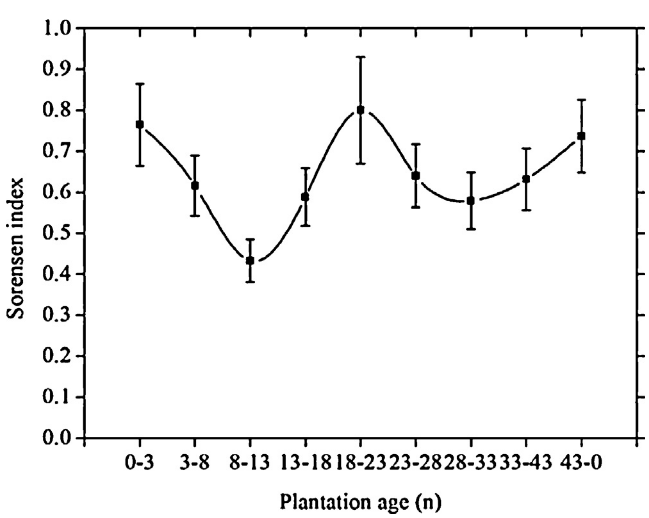


**Fig. 4.** The changes in the β-diversity of all species (shrubs and herbaceous species) with increasing plantation age in a desert steppe of China.

### 3.3. Changes in aboveground biomass and vegetation cover during succession

The aboveground biomass differed significantly among plantation ages for herbaceous species ($F_{2,7} = 31.14$, $P < 0.001$), shrubs ($F_{2,7} = 34.06$, $P < 0.001$), and the community as a whole ($F_{2,7} = 39.28$, $P < 0.001$) (Fig. 5). With increasing plantation age, the aboveground biomass of herbs, shrubs, and the overall community initially increased, reaching maximum values of 1314.68 ± 197.20 kg/ha in year 28, 5499.90 ± 824.98 kg/ha in year 18, and 6408.66 ± 1455.41 kg/ha in year 18, respectively; thereafter, they decreased gradually. The aboveground biomass of herbs, shrubs, and the community as a whole averaged 916.11 ± 133.67, 3715.00 ± 557.25, and 4631.11 ± 537.33 kg/ha, respectively. Based on significant quadratic regression equations for the three biomass

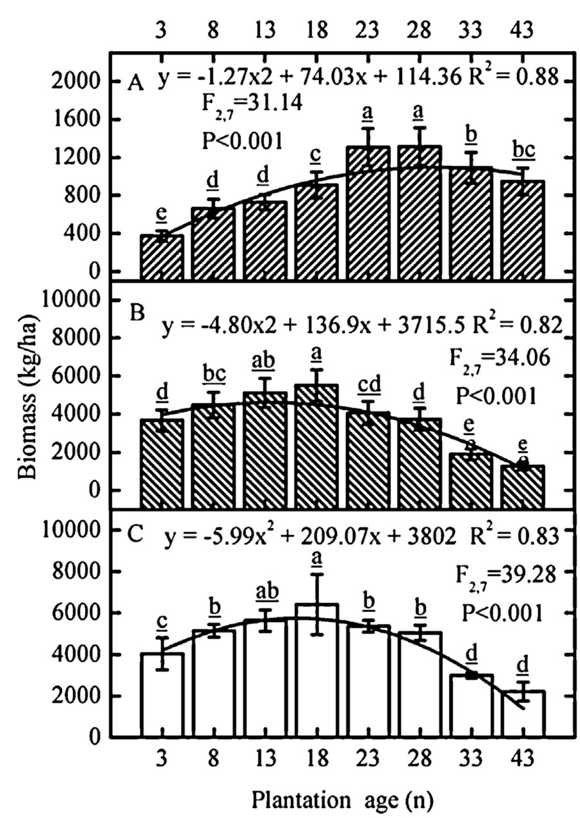


**Fig. 5.** The changes in aboveground biomass as a function of plantation age: (A) herbaceous species biomass, (B) shrub (and sub-shrub) species biomass, and (C) total community biomass. Means for a parameter followed by different letters differ significantly (Tukey's HSD, $P < 0.05$).

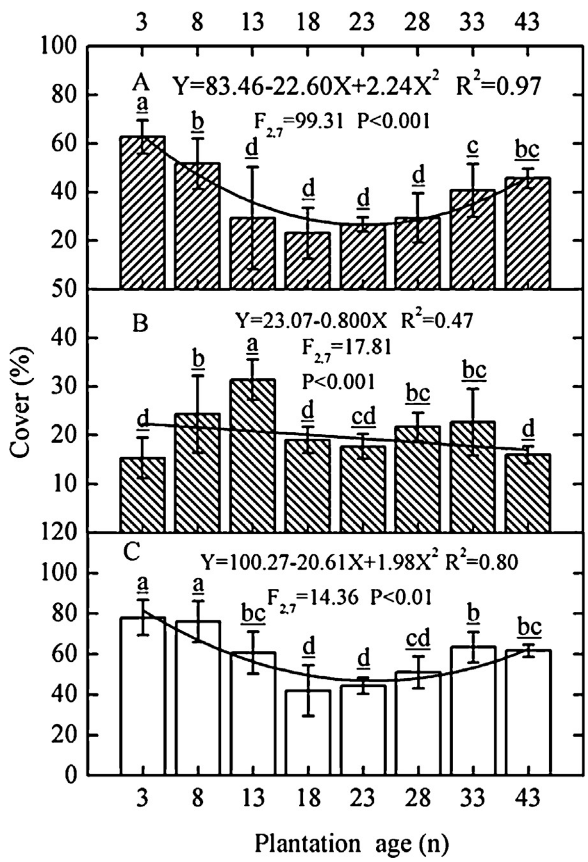


**Fig. 6.** The changes in vegetation cover as a function of plantation age: (A) Herbs, (B) Shrubs and sub-shrubs, and (C) the community as a whole. Means for a parameter followed by different letters differ significantly (Tukey's HSD, $P < 0.05$).

categories, shrubs had a greater contribution and accounted for 80.6% of the community biomass (Fig. 5). Overall, herb biomass followed the opposite of the patterns for shrub and community biomass.

Succession significantly affected the vegetation cover of herbs ($F_{2,7} = 99.31$, $P < 0.01$), shrubs and sub-shrubs ($F_{2,7} = 17.81$, $P < 0.001$), and the community as a whole ($F_{2,7} = 14.36$, $P < 0.01$) (Fig. 6). With increasing plantation age, the vegetation cover of herbs and the community as a whole followed a quadratic function, decreasing to minimum values of 23.1 and 42.1% in year 18, respectively. Based on a significant regression equation, herbaceous plants accounted for 64.8% of the total vegetation cover. In contrast, shrub cover fluctuated, with an average value of 21.1%, and there was a signficant decreasing linear trend as a function of plantation age ($R^2 = 0.47$).

### 3.4. Effects of the environmental variables during succession

The environmental variables significantly affected species composition, aboveground biomass, and vegetation cover (Fig. 7). The model accounted for 98.7% of the total variance along the first four axes during succession. Along axis 1, which accounted for 87.2% of the total variance (Table 3), plantation age had the strongest effect on the numbers of herb and shrub species ($P < 0.001$; Fig. 3). Soil crust thickness and soil type significantly affected total species in the community ($\tau > 0.45$, $P < 0.001$; Table 4), but were not significantly correlated with the numbers of herbaceous and shrub species. The soil crust thickness and soil moisture from 0 to 200 cm both significantly affected total community biomass ($\tau > 0.47$, $P < 0.01$), shrub biomass ($\tau > 0.46$, $P < 0.001$), and herb biomass (soil moisture only; $\tau = 0.63$, $P < 0.001$), and the total community vegetation cover ($\tau = -0.41$ and $\tau = 0.40$, respectively; $P < 0.001$) and herbaceous vegetation cover ($\tau > 0.46$, $P < 0.001$). The soil moisture in the 40- to 100-cm soil layer affected aboveground biomass and vegetation cover more strongly than soil moisture in the surface 40-cm soil layer or in the 100- to 200-cm soil layer (Fig. 7). The community, shrub, and herb biomass values were significantly positively correlated with longitude ($\tau > 0.45$, $P < 0.01$; Table 4). Community total vegetation cover and herbaceous cover were both positively correlated with soil bulk density ($\tau > 0.49$, $P < 0.001$), but were both significantly negatively correlated with soil crust thickness ($\tau < -0.40$, $P < 0.01$). However, shrub cover was only significantly affected by *CSI* ($\tau = 0.57$, $P < 0.001$; Table 4). However, latitude and slope aspect were not significantly correlated with any of the vegetation parameters.

## 4. Discussion

### 4.1. Changes in habitat characteristics during succession

Afforestation can greatly alter vegetation succession, which provided suitable microhabitats for the growth of herbaceous plants in degraded sandy lands (Liu and Zhao, 2009; Amici et al., 2012). As soil crusts gradually formed on the soil surface with the succession of vegetation and soil system, *CSI* ($F_{2,7} = 2.87$, $P < 0.05$) and the soil crust thickness ($F_{2,7} = 14.19$, $P < 0.001$) both increased remarkably, then gradually decreased (Fig. 8). Although soil crusts provide both benefits (a barrier to evaporation) and drawbacks (increased difficulty for root penetration into deeper soil layers) (Li et al., 2013), our study showed that soil bulk density ($F_{2,7} = 0.78$, $P > 0.05$) and soil moisture ($F_{2,7} = 84.54$, $P < 0.001$) decreased significantly (Fig. 8), because roots loosened the soil and soil moisture was consumed by plant growth. This means that the water balance changed during succession.

Although soil crusts reduce evaporation and can improve soil water availability in the shallow layers (Li et al., 2004; Wang et al., 2011), they can also significantly decrease rainfall infiltration because they intercept precipitation, thereby decreasing replenishment of water in deeper soil layers (Li et al., 2013; Zhang et al., 2014). During the early stages of succession, precipitation can infiltrate and reach deep soil layers, leading to higher soil moisture contents (Li et al., 2007; Liu and Zhao, 2009); however, our study revealed that the low water-holding capacity of the soils of mobile sand dunes mean that water in the surface 40 cm of the soil may drain rapidly into deeper layers, particularly when the soil crust is still thin. This may explain why the soil moisture content decreased significantly during succession by around 18 years after afforestation. The soil moisture decreased from 9.9 ± 2.8% in year 3 to 3.2 ± 2.0% in year 43 (Fig. 8). After 28 years, soil moisture content has basically stabilized at ∼3%. Therefore, the increasing thickness of the soil crust appears to have had an important influence on moisture in the surface soil and led to redistribution in soil water in the desert steppe of China.

### 4.2. Changes in community characteristics during succession

Changes in vegetation structure and in ecological processes during succession provide a high diversity of niches (Ruiz-Jaén and Aide, 2005; Jules et al., 2008; Suganuma et al., 2014), thereby facilitating the establishment of desirable species in later successional stages (Wright et al., 2009). The vegetation patterns are characterized by distinct patchiness, with the patches composed of shrubs and herbaceous plants in the semiarid desert steppe of China (Li et al., 2009; Lin et al., 2010). In our study, the life forms also change in response to these habitat changes, and the

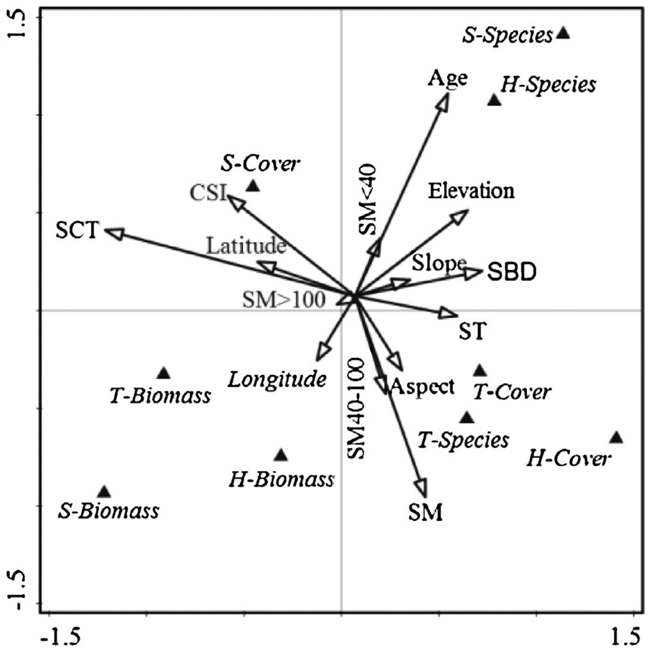


**Fig. 7.** Redundancy analysis (RDA) using data from all plantation ages combined for the relationship between the environmental variables and plant species composition, aboveground biomass, and vegetation cover. Definitions: Age plantation age; Aspect, slope aspect; Biomass, Community biomass (T-, total; S-, shrub; H, herb); Cover, vegetation cover (T-, total; S, shrub; H, herb); CSI, community stability index; SBD, soil bulk density; SCT, soil crust thickness; SM, soil moisture (<40, from 0 to 40 cm; 40-100, from 40 to 100 cm; >100, from 100 to 200 cm); Species, number of species (T-, total; H, herb; S, shrub); ST, soil type.

population of annual herbs generally decreased with widespread species loss such as *A. ordosica* and *A. squarrosum*, and have been gradually replaced by endemic species such as perennial herbs (forbs, grasses, and legumes) during succession. The perennial herbs reached a peak abundance when the heliophytes and mesophytes were both dominant, however, subsequently decreased due to increased dominance of ombrophytes, resulting in elimination of the heliophytes during later stages of succession.

Species diversity appeared to reach its maximum towards the middle of the succession, which supports the third hypothesis that we described in the Introduction (Aubert et al., 2003; Malacska et al., 2004; El-Sheikh, 2005; Zhu et al., 2009; Suganuma et al., 2014). The lower species diversity in younger successional stages was related to the high dominance of a few pioneer species, which is a common feature of secondary forests (Bu et al., 2014). In the semiarid desert steppe of China, shrub cover increased from 15.3 ± 2.1% in year 3 to 31.6 ± 4.2% in year 13 during succession, and the dune surfaces appeared to have stabilized (e.g., the community stability index increased from 3.53 ± 0.36 to 3.87 ± 0.54). Furthermore, the aboveground biomass first increased and then decreased during succession (Fig. 5), although the decrease occurred later for herbs. This means that the shrub structure evolved into a multi-synusium with a mixed shrub and herb community, and there is evidence that the vegetation community has gained some ability to self-regulate at this stage, supported by Li et al. (2009). However, with the increase of succession, the vegetation community will be to make the transition to the zonal vegetation, and gradually reach the climatic climax community in the semiarid desert steppe of China, for example, *Plantago asiatica* and *Oxytropis bicolor*, etc.

**Table 3**
The eigenvalues and intraset correlations for the RDA for the relationship between the environmental characteristics and the plant species composition, aboveground biomass, and vegetation cover.

| Parameter | Axis | | | | Total inertia |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | |
| Eigenvalue | 0.5043 | 0.2848 | 0.1105 | 0.067 | 0.9366 |
| Composition, biomass, and cover–environment correlations | 0.767 | 0.654 | 0.259 | 0.160 | |
| Cumulative percentage of variance | | | | | |
| For species composition, biomass, and vegetation cover | 50.43 | 78.91 | 89.96 | 93.63 | |
| For species composition, biomass, and the cover–environment relationship | 87.24 | 91.85 | 96.93 | 98.73 | |
| Sum of all eigenvalues | | | | | 1.000 |
| Sum of all canonical eigenvalues | | | | | 0.9366 |

**Table 4**
Kendall's tau (τ) correlation matrix between the environmental variables and plant species composition, aboveground biomass, and vegetation cover. *CSI*, community stability index; SCT, soil crust thickness; SM, soil moisture from 0 to 200 cm; SBD, soil bulk density; ST, soil type.

| | Number of | | | Biomass | | | Vegetation cover | | |
|---|---|---|---|---|---|---|---|---|---|
| | Total species | Herbaceous species | Shrub species | Total | Shrub | Herb | Total | Shrubs | Herbs |
| Plantation age | 0.04 | 0.61*** | 0.58*** | −0.14 | −0.26 | 0.51 | −0.27 | −0.10 | −0.14 |
| Longitude | −0.22 | 0.08 | −0.07 | 0.53** | 0.46** | 0.57*** | 0.03 | 0.11 | −0.05 |
| Latitude | 0.04 | −0.20 | −0.17 | 0.10 | 0.00 | 0.23 | -0.23 | −0.27 | −0.26 |
| Elevation | −0.17 | −0.01 | 0.08 | −0.07 | −0.16 | 0.19 | -0.03 | −0.01 | 0.05 |
| Slope | 0.28 | 0.25 | 0.31 | −0.01 | 0.08 | −0.10 | 0.14 | 0.16 | 0.12 |
| Slope aspect | 0.12 | −0.04 | −0.07 | 0.07 | 0.12 | −0.28 | 0.28 | −0.13 | 0.29 |
| CSI | −0.32* | 0.18 | 0.22 | 0.33** | 0.23 | 0.21 | −0.14 | 0.57*** | −0.19 |
| SCT | −0.46*** | −0.17 | −0.14 | 0.59*** | 0.47*** | 0.46 | −0.41** | 0.18 | −0.47** |
| SM | −0.02 | −0.12 | −0.16 | 0.48** | 0.55*** | 0.63*** | 0.40** | 0.18 | 0.48** |
| SBD | 0.06 | 0.24 | 0.30 | −0.07 | −0.07 | 0.08 | 0.53*** | 0.17 | 0.50*** |
| ST | 0.52*** | 0.10 | 0.17 | −0.19 | −0.15 | −0.09 | 0.04 | -0.21 | 0.10 |

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

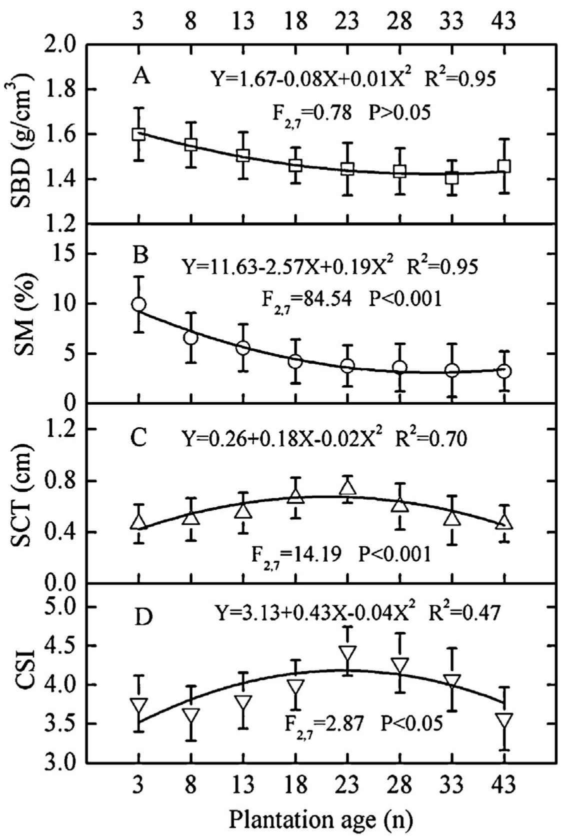


**Fig. 8.** Changes in four key environmental variables in a semiarid desert steppe of China as a function of plantation age. (A) Soil bulk density (SBD), (B) Soil moisture from 0 to 200 cm (SM), (C) Soil crust thickness (SCT), and (D) community stability index (*CSI*).

### *4.3. Ecological mechanism of afforestation succession*

Shrub diversity is affected by both environmental factors and the effects of afforestation-induced succession in arid and semiarid regions (Li et al., 2009). We find that soil crusts can not only control the distribution and abundance of many species, but soil type also affected species composition ($P < 0.001$; Table 4). For example, *Nitraria sphaerocarpa*, *Kalidium cuspidatum*, *Haloxylon ammodendron*, *Kalidium gracile*, and *Nitraria tangutorum* are commonly found in alkaline soils, and these conditions reduce the possibility of other species coexisting with these species (Liu and Zhao, 2008; Liu et al., 2011; Zhao and Liu, 2010). Similarly, the psammophytes *H. scoparium*, *C. korshinskii*, *C. microphylla*, *Calligonum mongolicum*, and *A. ordosica* survive well in habitats subjected to wind erosion and sand burial in areas with semi-mobile dunes, as has been previously reported by Liu et al. (2007) and Liu and Zhao (2012). However, for more cosmopolitan species, such as *O. aciphylla*, it is more difficult to determine the relationship between soil properties and species diversity (Li et al., 2009). This means that the changes in species diversity in our study support the hypothesis of Dodd et al. (2002), that dominance by shrubs or grasses is related to soil texture in a semiarid grassland.Theoretically, Li et al. (2013) find that soil moisture in the surface layer (0–40 cm) will affect the species richness and diversity of shallow-rooted herbs in semiarid and arid regions, while our study showed that water availability in the 40- to 100-cm soil layer played a decisive role in vegetation productivity and vegetationcover because a dry sand layer occurred between 20 and 40 cm. The importance of the deeper soil moisture can be partially explained by the fact that the distribution of the root systems of perennial herbs, shrubs, and sub-shrub, is concentrated in the 40- to 100-cm soil layer. Moreover, the dew had an important ecohydrological influence on herbs, especially for annual, ephemeral, and semi-ephemeral plants (Li et al., 2008, 2013), because it amounted to 37.9% of the total precipitation during a given period (Chen et al., 2007), which could reduce the dependency of these plants on soil moisture. The habitat heterogeneity that developed during succession changed the water balance, which can gradually increase species richness, vegetation cover, and biomass (Coppedge et al., 2008). The interactions between the vegetation development and the environmental factors could improve habitat conditions (Alrababah et al., 2007). These changes would make it possible for more species to survive and reproduce, and the level of interspecific competition (e.g., between heliophytes and ombrophytes) could simultaneously increase. The net effect of these processes will lead to preservation of some species and the elimination of others. In fact, species patterns was also affected by soil properties, scales and disturbances (Li et al., 2009), this will require further research in the future.

We also found that the plantation age, soil moisture and soil crust thickness significantly affected the number of families and

**Table 5**
Degrees of freedom and *F*-statistics for the repeated-measures ANOVA on the effects of the environmental variables and their interactions on the number of families, genera, and species, and on total community biomass and vegetation cover. Age plantation age; SBD, soil bulk density; SM, soil moisture; SCT, Soil crust thickness.

| Factor | df | Number of Families | Number of Species | Total community biomass | Total community vegetation cover |
|---|---|---|---|---|---|
| Age | 2,7 | 6.67*** | 9.81*** | 30.96*** | 15.72*** |
| SCT | 2,3 | 5.50** | 4.59* | 11.99*** | 5.27** |
| SM | 2,4 | 3.81* | 3.37* | 5.32** | 8.51*** |
| SBD | 2,3 | 2.52 | 0.07 | 0.63 | 4.38* |
| Age × SCT | 2,4 | 2.50 | 2.17 | 0.19 | 0.23 |
| Age × SM | 2,3 | 0.17 | 0.63 | 0.03 | 0.22 |
| SCT × SM | 2,3 | 3.55* | 1.35 | 0.55 | 1.10 |
| Age × SCT × SM | 2,6 | 2.23 | 1.09 | 0.45 | 0.56 |
| Age × SBD | 2,8 | 4.44* | 0.47 | 0.27 | 0.21 |
| SCT × SBD | 2,4 | 1.88 | 0.94 | 0.49 | 2.22 |
| Age × SCT × SBD | 2,7 | 1.09 | 0.87 | 0.45 | 1.12 |
| SM × SBD | 2,5 | 0.59 | 0.95 | 0.11 | 0.15 |
| Age × SM × SBD | 2,4 | 1.45 | 0.67 | 0.54 | 1.45 |
| SCT × SM × SBD | 2,4 | 1.67 | 0.45 | 0.67 | 0.43 |
| Age × SCT × SM × SBD | 2,4 | 1.74 | 1.87 | 1.35 | 1.25 |

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

species, and community biomass and cover, and the number of families had a significant relationship with the soil crust thickness × soil moisture interaction and the plantation age × soil bulk density interaction ($P < 0.05$; Table 5). Therefore, the interactional feedback between vegetation development, soil crusts and soil water appear to be an important driver of vegetation restoration in the sand-binding vegetation communities, and improving our understanding of these drivers will let us improve the strategies used to construct a sand-binding vegetation system and improve future ecological management in the semiarid desert steppe of China.

## 5. Conclusions

Afforestation effectively controlled desertification and environmental deterioration with the sand-binding vegetation in arid and semiarid regions, but its effects on biodiversity conservation has been debated among studies. This study showed that afforestation greatly affected the community and habitat characteristics, and promoted the formation of the crust on the soil surface with the succession of vegetation in the semiarid desert steppe of China. Soil crusts improved soil water availability in the shallow layers, but a dry sand layer between 20 and 40 cm provided the suitable microhabitats for annual herbs replaced by perennial herbs during succession. Simultaneously, the deep root shrubs had been decayed and replaced gradually by perennial herbs and sub-shrub that can be regenerated naturally, because soil crust significantly decreased the rainfall infiltration by intercept precipitation in deeper soil layers. The sand-binding vegetation community was composed of shrub and sub-shrub in the early afforestation, and gradually evolved a mixed community of sub-shrub and herb with the self-regulation during succession.The interaction between soil crust thickness and soil type significantly affected the number of families and species, while soil moisture especially for the 40- to 100-cm soil layer played a decisive role in vegetation productivity and vegetation cover. The dew could reduce the dependency of herbs on soil moisture, especially for annual, ephemeral, and semi-ephemeral plants. Therefore, the interactional feedback between vegetation development, soil crusts and soil water appear to be an important driver of vegetation restoration in the sand-binding vegetation communities, and this mechanism of the succession paradigm of afforestation was will let us improve the strategies used to construct a sand-binding vegetation system and improve future ecological management in the semiarid desert steppe of China.

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